THE

NEW PHYTOLOGIST,

A BRITISH BOTANICAL JOURNAL,

EDITED BY A. G. TANSLEY, M.A., F.L.S.,

UNIVERSITY LECTURER IN BOTANY, CAMBRIDGE,

ASSISTED BY THE STAFF OF THE CAMBRIDGE BOTANY SCHOOL.

VOLUME VIII.

PP X. AND 392.

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LOXSOMACEÆ.

As the order of the Loxsomaceæ contains only one species we may at once consider its affinity to the preceding orders of the phylum. The exarch solenostele of *Loxsoma* might well be derived from the simpler Botryopterideæ, especially if the latter were, as the writer believes, primitively exarch. The fronds of many members of the fossil order were, however, more complex, in that they branched in more than one plane. The sporangia of both orders differed strikingly in their disposition on the frond, and in the structure of the sporangial wall and annulus. Therefore, though *Loxsoma* may well be descended from allies of the Botryopterideæ it would be unwise to assert a direct affinity between it and the latter order.

Both Mr. Gwynne-Vaughan and Professor Bower admit that *Loxsoma* shows a certain relationship to the Hymenophyllaceæ, in which order it was formerly included; but they consider that it approaches closer to certain Cyatheaceæ (19). Professor Bower points out that the texture of its leaf, the dehiscence of its sporangia, their structure and low output of large spores, are against such an affinity; but he states that, putting aside the low output of spores, the Hymenophyllaceæ might have arisen from such a type as *Loxsoma*, and that in this connection the anatomy of its rhizome should be interesting (6). Since its rhizome is now known to be solenostelic the protostelic Hymenophyllaceæ cannot have been derived from *Loxsoma*. Further *Loxsoma* cannot be directly derived from filmy ferns, for its leaves are well developed. Both orders are clearly to be derived from protostelic forms, and these may have been in both cases exarch; but if, as has been asserted, the Hymenophyllaceæ are primitively endarch (2), (41), the exarchy of certain species of *Trichomanes* and *Loxsoma* is homoplastic and does not indicate close affinity. Since Professor Bower has shown that a basipetal succession of sporangia has arisen independently in several series of forms, this similarity may also be due to parallel development.

The most striking similarities between the Schizæaceæ and

Loxsoma, *viz.*, the solenostele and C-shaped trace are very common in the Ferns. The former certainly and the latter possibly originated independently in the two orders; but the exarchy of both may well have been inherited from an exarch protostelic ancestor.

Loxsoma Cunninghami, the only species of the Loxsomaceæ, has an exarch solenostele and a C-shaped leaf-trace. According to the views expressed by the writer the exarchy of its stele is the principal character in which *Loxsoma* is more primitive than the Gleicheniaceæ. Since the solenostele of *Gleichenia pectinata* was clearly evolved within the order it seems probable that both orders have been derived from protostelic forms of mainly Gleicheniaceous type, but with entirely centripetal wood. The principal changes which, on this hypothesis, have occurred in the evolution of a form like *Loxsoma*, *viz.*, the evolution of solenostely from protostely, of pinnate from dichotomous fronds, of the " gradate " from the " simultaneous " sorus, have been traced in several evolutionary series of forms and may be regarded as well established evolutionary processes (16), (24), (20), (36), (31), (6).

Solenosteles have been shown to have arisen very frequently in the Ferns; those of *Loxsoma* and of *Matonia* almost certainly originated independently, for it is clear that the ancestors of *Loxsoma* began to diverge from the Gleicheniaceous type before those of *Matonia* had acquired any centrifugal xylem. This is borne out by the considerable differences in the fronds and sori of *Matonia* and *Loxsoma*.

Loxsoma is perhaps most closely allied to the Cyatheaceæ and Polypodiaceæ. Mr. Gwynne-Vaughan has pointed out that anatomically the genus comes nearest to the more primitive members of these orders, to the simpler Dicksonias and Davallias (19). The similarity extends to the solenostely, to the structure of the leaf-trace, to the pinnate division of the fronds and to other less important points. Professor Bower recognizes this affinity not only in the anatomy, but also in the habit, the form of the indusium and the " gradate " sorus (6). But since *Loxsoma* is exarch the centrifugal wood of the Polypodiaceæ and Cyatheaceæ must (though these orders are in other respects very close to *Loxsoma*) have been developed since the two stocks began to diverge from one another.

OSMUNDACEÆ.

In the recent Osmundaceæ the centre of the stem is occupied by a pith, embedded in the periphery of which is a circle of woody strands, separated by medullary rays, through which the continuous ring of phloem may project slightly inwards. In a few species the

mature stem has an internal endodermis, and in *Osmunda cinna-
momea* a little internal phloem *may* occur at the branching of the
stem. Dr. Jeffrey and Mr. Faull assert that this internal phloem
is vestigial (17), (24), while Mr. Seward and Miss Ford regard it as
a relatively recent acquisition (39).

The inward projection of the phloem at the medullary rays is
quoted in support of the vestigial nature of internal phloem. So
is the presence, in certain species, of an internal endodermis,
coupled v ith the rarity of the ectophloic siphonostele among ferns,
and the f..ct that in *Platyzoma* and some Polypodiaceæ, this type
was clearly derived from a solenostele by loss of internal phloem
(43). Appeal is also made to an analogy with *Schizæa* and the
Ophioglossaceæ (17); but the evidence that these forms ever
possessed internal phloem is quite insufficient. Again, if internal
phloem is *in statu nascendi*, it must have arisen at the branching of
the stem ; but in those ferns in which its origin has been traced it
arises in the ontogeny, and presumably in the phylogeny, at the leaf-
gaps. Dr. Jeffrey claims that the mesarchy of the xylem and the
concentric structure of the leaf-trace favour the vestigial nature of
the phloem ; but, as Dr. Scott points out, both these characters
occur in protostelic forms, " . . . . so that it is difficult to see how
they affect the question " (37). Mr. Faull claims that if the internal
phloem of *Osmunda cinnamomea* is a recent acquisition, the stele of
this species would be very plastic ; this is true, but this plasticity
would appear to be just as great if the internal phloem were
vestigial. That every stage, except the complete disappearance of
internal endodermis, occurs in *O. cinnamomea* shows that the series
of forms connecting the extreme types is very complete, but does
not prove which end of the series is the more primitive.

Mr. Kidston's and Mr. Gwynne-Vaughan's recent researches on
the geological history of the Osmundaceæ, clearly show that the
older Permian members of the Osmundaceæ (included in the genus
Zalesskya) were protostelic, though the central tracheæ of some
forms had already become short and wide, functioning rather as
water-storers than as water-conductors (29). They have shown that
in the Jurassic *Osmundites Dunlopi* the centre of the stem is occupied
by a pith, abutting on a woody ring, unbroken by the departure of
leaf-traces (28). Their work seems to show that the Osmundaceæ
as a whole are descended from protostelic forms ; their results have
been widely accepted considering how recent is their publication
(43), (9). But Mr. Kidston and Mr. Gwynne-Vaughan have also
shown that *Osmundites skidegatensis*, from the Lower Cretaceous, is

typically dictyostelic, external and internal phloem being continuous through the gaps between the meristeles (28). Since the annular stele of the Osmundaceæ appears to have been at first unbroken by leaf-gaps they suggest that the internal phloem probably arose at the branching of the stem, as in *Osmunda cinnamomea*, and was continuous with the external phloem through a ramular gap, and that the connection of internal and external phloem through the leaf-gaps, as seen in *Osmundites skidegatensis*, is a later modification connected with the development of foliar gaps (29). The view that the internal phloem is a recent acquisition is also supported by the absence of an internal endodermis in young plants of *O. cinnamomea*, and by the absence of any correlative reduction of the leaf-trace in recent Osmundaceæ (43).

The fossil Osmundaceæ seem to be closely related to the Botryopterideæ. The protostele of *Zalesskya* recalls that of the simpler Botrypterideæ. This oldest Osmundaceous genus also approaches the simple *Tubicaulis* and *Grammatopteris* in that nearly the whole of the wood is centripetal, as it still is in *Todea hymeno-phylloides*. Most recent Osmundaceæ are endarch and the whole of the centripetal wood has been replaced by pith. This gradual development of the central wood as non-conducting tissue and the correlated acquisition of centrifugal wood had already been initiated in *Zalesskya*, where the central part of the centripetal xylem was no longer water-conducting and the protoxylem no longer absolutely peripheral. The multiseriate pitted tracheæ of the Botryopterideæ are found in the Osmundaceæ, and are confined among recent ferns to them and the Ophioglossaceæ (22). The structure of the Osmundaceous sporangium in which the annulus is a group of cells, also favours the hypothesis that the Osmundaceæ may have been derived from the simpler Botryopterideæ or from their near allies.

The Hymenophyllaceæ differ strikingly from the Osmundaceæ in the anatomy of their stems and fronds and in their sporangial characters, so that the assumption of a filmy habit by some Osmundaceæ and the occasional production in this order of sub-filamentous prothalli are clearly due to development parallel to the Hymenophyllaceæ.

The discovery of *Zalesskya* has brought the Osmundaceæ nearer to *Lygodium*, the most primitive of the Schizæaceæ, though the exarch homogeneous stele of the latter genus appears to be more primitive than the stele of *Zalesskya*. The writer cannot agree with Dr. Campbell, who regards the Schizæaceæ as the nearest relatives of the Osmundaceæ (13). The structure of their

A THEORY OF ALTERNATION OF GENERATIONS IN ARCHEGONIATE PLANTS BASED UPON THE ONTOGENY.

By William H. Lang, M.B., D.Sc.,

Lecturer in Botany in the University of Glasgow.

I T is difficult to overestimate the importance of the regular succession of two generations, differing both in their vegetative and reproductive parts, in all plants from the Bryophyta upwards. The clear recognition of this by Hofmeister rendered possible the accurate study of the morphology of these plants and we are now in possession of the main descriptive facts regarding the life-histories of nearly all the groups. A copious literature has also accumulated on the nature of this alternation of generations, and the proper understanding of this must have a far-reaching influence on morphology as it passes from the purely descriptive stage.

I do not propose to summarise here even the most recent works dealing with the nature of alternation. In his address to the Botanical section of the British Association in 1896, Scott restated the theory of homologous alternation of generations; he held this to be another hypothesis " equally worthy of verification " and an alternative to the antithetic theory of Celakovsky and Bower. Since that date a number of investigators have discussed the nature of alternation, and advanced views as to its origin. The names of Campbell, Coulter, Klebs, Potonié, Hallier, Lignier, Tansley, Schenk and Goebel may be mentioned without citing the literature in detail. We may, however, recognise several broad lines on which speculation has proceeded.

In the first place we have the antithetic theory, the essential feature of which lies in its recognition of the spore-producing generation as an interpolated phase in the life-history, originating in post-sexual complications, and in its not regarding this generation as derived by the modification of a generation resembling the sexual one. On this theory the spore-producing generation has had a history on lines of its own, which are suggested by such a series of forms as *Oedogonium, Coleochaete, Riccia*, the more complicated sporogonia of the Bryophyta, and the sporophyte of Pteridophyta. These are recognised by the advocates of the antithetic theory as not phyletically related.

The alternative view that the spore-producing generation in Bryophyta and Pteridophyta is strictly homologous with the sexual generation, and that the alternation in these groups differs only in its regularity from the succession of sexual and asexual forms in many Thallophyta, was advanced by Pringsheim, and, as mentioned above, restated by Scott. The homologous theory in this form was not applied in detail to the origin of the sporophyte, as we find it in Bryophytes and Pteridophytes, nor to the tracing of particular homologies between the two generations.

The theories of Potonié, Lignier and Tansley, while differing widely among themselves, agree in asserting the homology of the two generations. In speculating on the origin of the sporophyte of Pteridophyta they make use of wide comparisons with the organisation of the gametophyte in other groups, especially in the Brown Algæ and Liverworts.

The three classes of theories which have been distinguished above may all be termed purely phylogenetic. In all of them little or no account is taken of the relations between the two generations in the ontogeny, and the comparisons with the gametophyte which are made (*e.g.* by Tansley and Lignier) in order to throw light on the morphology of the sporophyte frequently omit any consideration of the gametophyte of the particular form in question, and certainly attach no special importance to this.

A comparison between the two generations in *Lycopodium cernuum* was made by Treub in 1884, and is referred to by Scott in his address. A provisional and rather crude hypothesis of the origin of a homologous spore-bearing generation in the Ferns, advanced by the author in 1898, was based on comparison of the two generations in that group in the light of the facts of apogamy. Recent work indicates that the special significance of comparisons between the two generations in the same group is being more

widely recognised.   The references to the origin of alternation of generations by Schenck[1] and by Goebel[2] may be specially mentioned, since some of the views elaborated below are clearly stated by these investigators, though not developed in detail.

It is remarkable that physiological works, even when dealing expressly with the causes of specific shape and the nature of ontogenetic development, have given little consideration to the special problems raised by the life-history of most plants consisting of two alternating generations.   This important aspect of the question of the transmission of characters and the explanation of ontogeny has doubtless not been emphasised because the development of the flowering plant can be experimentally treated as if it were as straightforward as that of a higher animal.   In reality the alternation requires to be taken into consideration here, just as it more obviously does in the case of the Fern or the Bryophyte.

The point of view which gives special weight to the comparison of the two generations in the same plant, or limited group of plants, may be contrasted as ontogenetic with the comparisons between the sporophyte of the vascular plants and the gametophyte of other and very distantly related groups, which form the basis of the hypothesis of Lignier, and of others already mentioned. These have been classed above with the purely phylogenetic theories.   The importance of concentrating attention upon the ontogenetic aspect appears to me to lie in the possibility that it leads to a working hypothesis which will supersede the antithetic and homologous theories as at present stated, and be fruitful in suggesting new lines of investigation into the subject.   Perhaps the most important of these lines are those on which the theory may to a certain extent be experimentally tested.

With this very general reference to the work of other investigators I propose to consider briefly what appear to me the most important facts bearing on alternation and to follow out what is implied by some assumptions that we are forced to make. On these I shall venture to outline a working hypothesis, based primarily on the facts of the ontogeny, as to the origin of the alternation in Bryophyta and Pteridophyta.   So far as I know the views to be expressed differ as a whole from any that have hitherto been stated, but it should be pointed out that practically all the facts

[1] Ueber die Phylogenie der Archegoniaten und der Characeen. Engler's Botan. Jahrbuch. Bd. XLII., Heft I., 1908.

[2] Einleitung in die Experimentelle Morphologie der Pflanzen, p. 199, &c.

and many of the deductions that go to form the hypothesis can be found in the works of one or other of the authors named. The facts are indeed matters of common knowledge, and repeated reference to the more or less real similarity of the views taken here to those already expressed by other investigators would prevent a brief and clear statement being made. It seems better to simply state for what it is worth the view of alternation to which I am led.

It is necessary to start with some general considerations on the nature of ontogeny, but we can avoid entering into the details of particular hypotheses of heredity. The general view of the organism and of its development from the germ-cell, which we are practically forced to take in the case of plants, is that all the cells resulting from the division of a germ-cell are potentially similar, and any one of them might reproduce the organism. The prevalence of vegetative reproduction, which, even in highly complex organisms, may start from a single somatic cell, indicates this. The development of the body of an organism from the germ-cell is regarded as due (*a*) to the properties of the germ-cell and (*b*) to the conditions under which the germ-cell develops. The conditions of development in the case of complex multicellular bodies are partly external and partly internal, the latter including the important factors of correlation and of the influence of one stage in the ontogeny upon the succeeding one. We thus arrive at the concept of a specific cell corresponding to each specific form, to which under normal conditions it gives rise.

In organisms without any alternation of generations there is only one type of body,[1] and any germ-cell, whether sexually or asexually produced, can be regarded as a specific cell with the power of giving rise under the proper conditions to a new individual like the parent. We have, however, to apply the concept of a specific cell to organisms with a definite alternation of generations. In these we meet twice in the life-cycle with a germ-cell, *i.e.* a cell capable of developing into an organism. These two germ-cells are the spore and the fertilised egg. The result of development of these two cells may be closely similar or widely different. The question at once presents itself, how are we to regard the ontogeny in these cases, and what do we understand by the specific cell of such an organism ?

Recent work has shown that in certain Algæ (*Dictyota, Poly-*

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[1] The word " body " is here used to denote the vegetative organs of an organism, or of either generation of an organism, in contrast to the reproductive organs.

siphonia) we appear to have an alternation of generations strictly comparable to those in archegoniate plants. Certain individuals bear the sexual organs, and from the fertilised egg, or its equivalent, a distinct generation is produced. In the form and organisation of the body the plant of this generation is almost exactly like the sexual plant, but its cells have nuclei with twice the number of chromosomes and the reproductive organs are different. The reproductive cells of this second generation arise by the division into four of a cell; in this division the number of chromosomes is reduced to one half, so that the spore has the same number of chromosomes as the sexual plant to which it gives rise. The alternation in these Algæ is thus antithetic in the sharp cytological differentiation between the two generations, but indications are wanting to show that the sporophyte has here had the history of gradual interpolation, which I take to be the essential of the antithetic theory as applied by Bower and Celakovsky to the origin of the sporophyte in archegoniate plants. The body of the sporophyte appears indeed to be strictly homologous with that of the sexual plant.

In the Liverworts, Mosses and the various groups of the Vascular Cryptogams we also find two generations, which regularly alternate. The one reproduces sexually and its cells have the half number of chromsomes: the other reproduces by spores and its cells have the double number of chromosomes. The two germ-cells, as in the Algæ referred to, are the spore and the fertilised egg, but here their products are very different, not merely in their reproductive organs but in the form and structure of their bodies.

In seeking for an explanation of the great differences between the alternating generations which are characteristic of the Bryophyta and Pteridophyta it is evident that there are two possible views :—

(*a*) That the germ-cells are so different that they necessarily give rise to bodies of different structure.

(*b*) That the two germ-cells alike represent specific cells of the plant, but that the conditions under which they develop are so different that two very unlike bodies result.

If we adopt the first view we have to regard the spore and fertilised egg as two profoundly different modifications of the specific cell. We are practically dealing with two specific cells (one for the sexual and one for the asexual generation), each of which has latent within it the characters of the other generation. On the second view the germ-cells would be essentially alike, the

different products of their development depending on the different conditions. It will be evident that the former view, if faced fairly, complicates the problem of the transmission of characters and that we should be on simpler lines if we could regard the specific cell as essentially similar throughout the life-history.

We know that the fertilised egg and the spore do differ in one normally constant and recognisable respect, that the spore (and the generation derived from it) is haploid, while the fertilised egg (and the generation derived from it) is diploid. When this was first recognised the tendency was to see in this difference the cause of the difference in the two generations, that is to regard them in the first of the two ways distinguished above. Recent work has tended to make this position very doubtful. On the one hand, as we have seen, there are organisms with the cytological difference between the two generations, but, with little or no difference in the bodies of the sexual and spore-bearing organisms. On the other hand in certain deviations from the normal life-cycle in Ferns the distinct body-forms of the prothallus and fern-plant may appear, although the cells are throughout haploid or diploid. The question has been discussed by Farmer and Digby, who conclude that " any cell the nucleus of which is provided with the necessary chromosomes, whether these are in single or duplicate number, is at least potentially endowed with the capacity of forming the starting point of the entire life-history, in so far as the grosser morphological characters are concerned." What does appear to be necessarily associated with the cytological difference is the mode of reproduction, sexuality in the haploid, and spore-production in the diploid generation. In this respect the similar bodies of *Dictyota* differ just as do the unlike bodies of the two generations in the archegoniate plants.

We seem therefore entitled to assume that the haploid and diploid germ-cells have potentially the same morphogenetic properties, *i.e.*, that under the same conditions they would give rise to similar bodies. This brings us to consider the second explanation of the difference of the two generations in Bryophyta and Pteridophyta, *viz.*, that it is due to the different conditions to which the germ-cell is exposed, in initiating the two generations. We have to enquire whether such a difference of conditions exists as may be assumed to account for the very different results.

There is normally a great difference in the conditions under which the spore and the fertilised egg commence their development in all archegoniate plants. The spore develops free, in direct

relation to the soil, water, light, etc.   The fertilised egg, on the other hand, develops in relation to the body of the sexual genera- tion.   It thus develops, under profoundly different conditions from the spore, firstly in that it is removed from all the influences acting on the spore, and secondly in that it is exposed to a new set of nutritive and correlative influences proceeding from the maternal body. We know practically nothing of the nature of these influences, but we can appreciate their existence and importance.   When we are able to change the conditions of development of an organism experimentally we are able to effect considerable changes in its form and structure, but in no case are we in a position to alter the conditions so fundamentally as is done in the case of a germ-cell developing within the tissues of the parent organism instead of as a free cell.

In the case of the spore-producing generation of Bryophyta this removal from external influences and exposure to the maternal influence of the sexual generation last practically throughout the development of the sporogonium.   In the Pteridophyta the sexual generation ultimately becomes free from the prothallus.   In all cases however the development is initiated and has advanced to the establishment of the various organs of the sporophyte under the maternal influence.   We are justified in assuming from some particular cases which have been studied that each stage in the ontogeny is determined by the preceding stage.   If therefore, as in the Pteridophyta, the first steps of development have taken place under the influence of the prothallus, the influence of the preformed parts of the young sporophyte may be legitimately assumed to exercise a "formative induction" on the further course of its development.

It may be noted in passing that these considerations on the influence of the enclosing parent generation on the enclosed stage, which is at the same time removed from the direct influence of the external environment, are capable, to some extent, of application also to the converse relation of the asexual and sexual generations in the seed-plants.   Here it is the gametophyte which develops enclosed within the body of the sporophyte.

In both these cases of parental association the direct influence of the retained organism on the part enclosing it must also be considered. The comparison with gall formation, due to the influence of an insect egg or larva, is here very suggestive. The development of the calyptra enclosing the sporogonium of *Aneura* or *Anthoceros* for instance may be regarded as a sort of gall due to the presence

of the growing young sporogonium.   A similar view may perhaps be taken of the ovule and seed.

We may now proceed to apply the point of view to which we have been led from a consideration of the relation of the two generations in the ontogeny to the phylogenetic problem of the origin of the two generations as we find them in the Bryophyta and Pteridophyta.

The question of the origin of the alternation of similar genera- tions as found in *Dictyota* and *Polysiphonia* may be dismissed as not falling within the scope of the present enquiry.   Recent inves- tigations have shown that important light may be expected on this question as our detailed knowledge of the types of alternation in the various groups of Algæ increases. Without suggesting that any particular form among the existing Algæ was an ancestor of the archegoniate plants, the origin of the latter may, in the light of our present knowledge, fairly be assumed to have been from forms in which a sexual (haploid) and asexual (diploid) generation of similar form alternated regularly.   The origin of the two generations in Archegoniate Plants need not now be sought in a differentiation of forms bearing, according to the external conditions, sexual or asexual reproductive organs on the same individual.

The development of the individual from the fertilised egg within the body of the parent individual would result from the egg remaining in the organ in which it was formed and being sought out and fertilised there by the motile spermatozoid. The association of the fertilised egg with the maternal body would give the pos- sibility of the latter influencing the developing zygote physiolo- gically.   The change from the extruded to the detained ovum may well have coincided with the departure from a purely aquatic mode of life.   At least it would have suited this departure.   The relation between the spread of organisms to the land and the origin of alternation as we see it in the archegoniate plants was first clearly pointed out by Bower.   It applies equally to a homologous theory, but it should be noted that the relation suggested here is rather a result of the terrestrial life than an adaptation to it.   Once the dependent relation of the diploid generation was established, pro- found and probably sudden changes might be expected to follow, resulting in the difference in body form between sporophyte and gametophyte.

It is probable that the spread to land would lead to the association of the two generations in more than one set of organ- isms, whether at the same or at different geological periods. The

association of the two generations may thus have been independent in the various groups of the Bryophyta and Pteridophyta. This is a matter for enquiry in each case and may be regarded as a quite open question. The modification of the attached generation may thus have been from the outset on different lines in the Bryophyta and Pteridophyta, or in the groups of the latter, such as the Lycopodiales and Filicales. A polyphyletic origin of the groups of archegoniate plants would probably involve great differences in the sporophytes from the outset, partly because of the differences of the retained specific cells, but also because the substratum formed by the sexual generation which influences the retained cell would be different in each case.

The germ-cells of the diploid generation, *i.e.* the spores, are assumed to have continued to be shed freely from the plant, though now provided with walls (if these were wanting in the ancestral forms) and adapted to aerial dispersal. They would serve as the means of spreading the organism to a distance.

On this hypothesis, the two generations in each species are regarded as homologous, in that they correspond to regularly succeeding individuals (sexual and asexual), developed from germ-cells which are similar in their morphogenetic powers. The degree of homology which can actually be traced in the vegetative structure of the individuals of the two generations is a matter for special enquiry in each case. It may range from practically complete identity as in *Dictyota*, to cases in which the development of the dependent generation is from the first so different to that of the free-living one, that the tracing of homologies between the bodies of the two forms is out of the question. Extreme examples of the latter case, such as the sporogonium of *Riccia*, have formed important links in the arguments for an antithetic origin of the second generation.

As regards the number of chromosomes in the nuclei and the mode of reproduction, the two generations are assumed to have been different in the ancestral forms. The asexual reproductive organs may, however, have been homologous with the sexual organs in these. Homologies, may therefore be looked for between the reproductive organs of the two generations of the same plant in the Bryophyta and Pteridophyta.

The further evolution of the organisms with definite alternation of unlike generations would involve the occurrence of variations and their selection. Without entering into the question fully, it should be pointed out that any variation must be assumed to affect the

specific cell. Whether the change in the specific cell is manifested in one or both generations, will depend on the conditions necessary for this being present. These conditions may be fulfilled in the one ontogeny and not in the other. The equivalence of the two germ-cells and the homology of the two generations in each species, does not preclude the occurrence of changes in the form and structure of the sporophyte, while the corresponding gametophyte remains apparently unaltered.

The hypothesis which has now been outlined may be termed an *ontogenetic theory of alternation* to distinguish it from other theories, since it specially depends upon a critical consideration of the ontogeny of both generations of the organism. In its phylogenetic application it is a theory of homologous alternation, though not inconsistent with some of the facts associated with the antithetic theory. The theory has, for the sake of clearness, been stated with as little qualification as possible and without reference to special cases. The assumptions that have been made of the equivalence of the specific cell in the two generations, of the importance of the changed conditions of development of the fertilised egg, brought about by its relation to the maternal body, and the probability of such an association having taken place once or oftener in an early stage of the evolution of land forms, are none of them forced. If granted they appear to place the relation of the two generations in a new light.

The test of any hypothesis of alternation lies in the degree to which it fits naturally with the detailed facts and explains them. I postpone to later papers any full discussion of the application of this ontogenetic theory to the great groups of the Bryophyta and Pteridophyta. These in the first place must be considered severally on the assumption that they may have been distinct in origin. This will be generally granted as probable for the Bryophyta and Pteridophyta, and the possibility of independent origin must be extended to the main phyla within these great groups.

In applying the hypothesis outlined above, it should be noted that the really important comparisons are between the gametophyte and sporophyte of the same plant, or within the same group. Such wide comparisons between the two generations as have been made, *e.g.*, between the sporophyte of Ferns and the gametophyte of Liverworts, may sometimes afford helpful analogies, but are as likely to be misleading. The objection to them is not that they are between sporophyte and gametophyte, but that they are between distant, and probably unrelated, forms.

It will be useful in conclusion to anticipate the detailed application of the theory, by a very brief survey of the broad features of the two generations in the three great groups of homosporous Vascular Cryptogams in which the life-history is known, the Ferns, the Lycopods and the Horsetails.

It is a remarkable fact that the general form of the prothallus is very uniform throughout the Ferns. This is important because we have in this group a wide ground of comparison, which is lacking in the homosporous Lycopods and in the Equisetaceæ. The flattened form with a distinction of midrib and wings, the occurrence of occasional dichotomous branching and less commonly of definite lateral lobing, and the position of the sexual organs on the under surface are characteristic. There is a considerable body of evidence from various sources, which points to the possibility of instituting a comparison between the fern leaf and a complete branch or branch-system of the fern prothallus. I shall not enter here into the bearing of this on the nature of the axis in the fern sporophyte, but it appears that it is in the comparison of the fern prothallus and fern leaf, that the homology between the two generations is most apparent in the group. The sporangia may perhaps be regarded as corresponding to the sexual organs on the prothallus, and in support of this the correspondence in position and the parallel in the various groups between the antheridia and sporangia in bulk and mode of development may be pointed out. On this view the sporophyte of the fern would be primitively megaphyllous and composed of a system of structures, each of which is comparable to a more or less branched fern prothallus.

The prothalli of the Lycopods and *Equisetum* differ in important details which need not now be considered. They resemble one another, however, and differ from the fern prothallus in one respect which has hardly been given the weight it deserves. I have elsewhere given my reasons for regarding the green prothalli of the type of *Lycopodium cernuum* and *L. inundatum* as relatively primitive in the Lycopodiaceæ. These and the prothallus of *Equisetum* consist of a main portion bearing definite lobes, which are developed in regular succession on the upper surface, and are not merely marginal. These lobes are most strikingly seen in large, well-grown prothalli. The sexual organs may be seated at the bases of these lobes in more or less regular relation to them. It is an equally striking and characteristic feature of the sporophyte in both these groups that the leaves are small in proportion to the stem and are often simple.

A comparison of the prothallus and plant in *Lycopodium* was

made long ago by Treub. The peculiarities of the Lycopodiaceæ have also led Lignier to suggest that their leaves are of a different nature to those of the Ferns. He distinguishes them as "phylloides" and compares them with amphigastrial scales of the thallus of his hypothetical pro-hepatic type.

While the particular comparison made by Lignier appears to me to be open to serious objections, I am led by the comparison of the two generations to a similar conclusion as to the difference between the leaves of the Lycopods and the Ferns. I should incline to regard the leaves of the sporophyte of the Lycopods, and also the leaves of the Equisetales, as corresponding to the assimilating lobes of the prothallus in the respective groups. This amounts to regarding both these groups as primitively microphyllous, but is not inconsistent with branching and the attainment of a considerable size by the leaves. The morphology of the two generations in these groups, contrasts with that of the prothallus and sporophyte of the Fern.

The brief general application of the ontogenetic hypothesis of alternation to the Vascular Cryptogams, which has been made in the last paragraphs, is of course quite provisional, and will require to be considered critically, at greater length and in greater detail. It will serve to suggest, however, that the broad comparison of sporophyte and gametophyte within the same group on these lines points to conclusions which agree with the important distinction on anatomical grounds of the Lycopsida and Pteropsida and with speculations based on other evidence. The hypothesis finds support in the facts which present most difficulty on an antithetic or on a monophyletic homologous theory.

Direct evidence on any view of the origin of the alternation of generations in archegoniate plants must from the nature of the case be slight. It may be claimed for the ontogenetic hypothesis advanced above that it brings into prominence the important factor of the different conditions of the ontogeny of the two generations and that it will lead to work on new lines and is open to experimental test. Experiment may not, as has been objected, be able "to reconstruct history," but it may show whether the two generations in the complete life-cycle are the results of equivalent germ-cells developing under different conditions, as is here suggested, or not.

fronds is very unlike, and Professor Bower's view that the Schizæa-
ceous annulus is a modified " ring" seems preferable to Potonié's
suggestion that it was originally a group of cells, in which case it
might be compared to that of the Osmundaceæ (31).

The mesarch protostele of the oldest Osmundaceæ recalls the
structure of *Gleichenia,* but both protostely and mesarchy are not
uncommon among the primitive ferns. The differences in their
fronds and sporangia seem to show that though both are relatively
primitive orders their common ancestor must lie a long way back.

Though both Matonineæ and Osmundaceæ are true Ferns,
there can be little question of a close affinity between forms so
unlike in their anatomy and soral characters.

The Cyatheaceæ, Polypodiaceæ and Loxsomaceæ are also
clearly very remote from the Osmundaceæ. The dictyostely of
Osmundites skidegatensis certainly vividly recalls the stelar structure
of many Cyatheaceæ and Polypodiaceæ, but it has been shown that
it probably arose in a different way from the dictyostely of these
two orders. The sporangia of the Osmundaceæ also differ in mode
of origin and in the structure of the annulus from the three other
orders mentioned.

SALVINIACEÆ.

The order of the Salviniaceæ only contains the highly modified
heterosporous and aquatic genera, *Salvinia* and *Azolla.* The
obviously reduced stele consists of a small strand in which the
first-formed elements are said to be central, though the xylem
appears to develop somewhat irregularly (33). The leaves of *Azolla*
are divided into dorsal and ventral lobes. Those of *Salvinia* are
arranged in whorls of three ; the dorsal leaf of each whorl is uni-
fascicular and undivided, while the others are modified to serve as
roots. The so-called sporocarp consists of a sorus completely
enclosed in a coherent indusium. The megasporangium contains
eight or sixteen spores. The gametophyte, especially the male
prothallus, is much reduced.

It is chiefly in their endarch protostely and the branching of
their fronds in a dorsiventral plane that the Salviniaceæ recall
certain Botryopterideæ. The writer, however, believes that the
endarchy is in both cases secondary ; in the Salviniaceæ it may be
due to reduction of the stem. The different structure of the
sporangia and the fact that the Botryopterideæ disappear in the
Permian, while the Salviniaceæ are not certainly recorded before
the Tertiary rocks, make it unlikely that there should be a direct
connexion between the two orders.

Dr. Campbell urges that the similarity between the development of the reniform leaves of some Hymenophyllaceæ and the leaves of the Salviniaceæ, and the absence of secondary roots in species of *Trichomanes* and *Salvinia* suggest an affinity between these two orders (13). The latter resemblance is clearly due to parallel development, for the less reduced species of both genera possess secondary roots. The fronds of both orders are reduced, though in different ways; the relatively thick leaf of the Salviniaceæ could hardly be derived from a filmy frond, since it is exposed to an even greater extent to the damp conditions that induce or are associated with the filmy habit. There is, however, a certain resemblance in the structure of the sori of the two orders and in their endarch protostely. Even if the Hymenophyllaceæ are primitively exarch the Salviniaceæ may have been derived by reduction from the modified endarch forms. But they may equally well have lost their definite and originally peripheral protoxylem owing to slow growth and reduction of the stem, the xylem then developing irregularly and somewhat centrifugally.

It is hardly necessary to point out that the Salviniaceæ show little, or no, resemblance to the Schizæaceæ. In respect of the soral distribution of their sporangia the Gleicheniaceæ come slightly nearer to the Salviniaceæ, but even they are very different. The Matonineæ, Cyatheaceæ, Polypodiaceæ, Loxsomaceæ and Osmundaceæ are all, in their various ways, so complex, and *Salvinia* and *Azolla* are so reduced, that it seems hopeless to trace any close affinity between the two latter genera and the other orders. Thus, though the Salviniaceæ clearly originated from homosporous leptosporangiate Ferns, their exact origin is obscure.

MARSILEACEÆ.

The Marsileaceæ are reduced, heterosporous, solenostelic Ferns. Mr. Johnson claims that the "sporocarp" enclosing the sori is of indusial nature, and that it and its stalk are "homologous with the petiole only of the sterile branch of the leaf" (25), (26). Dr. Campbell regards the sporocarp as made up of infolded and coherent leaflets (13). Mr. Johnson relies chiefly on the sequence of divisions in the segments of the apical cell, but this does not appear to be a reliable index of morphological value (9), (35). Further the branching and course of the vascular bundle of the peduncle on entering the sporocarp suggest that the latter is a lobed leaf rather than an indusium (13), (34).

The most important point in which the Marsileaceæ recall son e Botryopterideæ is the branching of the fertile frond in a dor c

ventral plane. The adaxial position of the sporocarp, may, however, be secondary, for Mr. Johnson has shown that it arises marginally on the leaf.

The Hymenophyllaceæ show few indications of affinity to the Marsileaceæ, but Dr. Campbell has recently suggested that the latter may have been derived from the Schizæaceæ (13), (14). The sporocarp is compared to the fertile pinnæ of *Aneimia*, and since it arises marginally, the comparison is a fair one. Other similarities mentioned are the solenostely, the dichotomy and dichotomous venation of the leaves, the shape of the sporangia, and the presence in the Salviniaceæ of what appears to be a non-indurated apical annulus. The further comparison of the simple leaves of *Pilularia* and *Schizæa pusilla* is hardly legitimate, for both are clearly secondary for their respective orders. In spite of the non-soral condition of the sporangia of the Schizæaceæ, the Marsileaceæ may be derived from the former if their solitary sporangia represent reduced monangic sori; in this case the Marsileaceæ were presumably descended from ancestors of the Schizæaceæ in which this reduction had not taken place.

Neither the Gleicheniaceæ, Matonineæ or Cyatheaceæ appear to be closely related to the Marsileaceæ, but as the Tree Ferns and the Polypodiaceæ appear to have had a relatively recent common origin, and as there is at least a possibility that the Marsileaceæ are descended from the Polypodiaceæ, it may be that the Cyatheaceæ are not as remote from the Marsileaceæ as might be supposed from the much greater development of their stems and fronds. Dr. Campbell, in the first edition of his " Mosses and Ferns," suggested that *Ceratopteris* might be intermediate between the Polypodiaceæ and Marsileaceæ, a view withdrawn in the second edition in favour of the Schizæaceous affinities of the latter. But even if we discard *Ceratopteris* as a link on account of its solitary sporangia and polycyclic dictyostele, it is still possible to derive the Marsileaceæ from the simpler, solenostelic Polypodiaceæ. The leaf-trace is fundamentally of the same type, and the " mixed sorus " is only known in these two orders. But in spite of these similarities an origin from the Schizæaceæ seems at least equally probable.

The Marsileaceæ also show a certain, though a less marked, resemblance to *Loxsoma*. In this genus the sporangia of a sorus arise in basipetal order; Professor Bower, however, has shown that ste ɪ a type of sorus gave rise more than once to a " mixed sorus." *oxsoma* appears to be closely related to the Polypodiaceæ, it is is d ral that forms similar to the latter should resemble the former. eler

There is little affinity between the Osmundaceæ and the Marsileaceæ, but the latter and the Salviniaceæ are usually classed together as the Hydropterideæ. Though both are aquatic and heterosporous ferns they differ considerably. The Salviniaceæ are anatomically simpler; their sporocarps appear to be indusial structures, not homologous with those of the Marsileaceæ, which consist of metamorphosed leaf-segments. In the latter order the sori are bi-sexual, in the former unisexual. Mr. Arber has pointed out that the heterospory of the Hydropterideæ originated independently of the heterospory that preceded the evolution of a seed (1). The differences between the Salviniaceæ and Marsileaceæ seem, however, not to exclude the possibility that heterospory originated independently in each order. Though Dr. Campbell does not expressly assert such an opinion, it should be noted that he derives the Salviniaceæ and Marsileaceæ from different homosporous orders (13).

PSARONIEÆ.

The Psaronieæ are fossil stems from the Upper Carboniferous and Permian rocks. In the simplest species, *Psaronius Renaulti*, the stem contains a single solenostele. This is presumably the most primitive form of the order (38). The other species are dictyostelic and polycyclic, each circle of strands acting as a compensation system to the one immediately outside, and thus eventually repairing the leaf-gap. Some species also possess peripheral steles; these anastomose with the other steles, but do not contribute to the formation of leaf-traces. The traces of adventitious roots are given off from them. Since these peripheral steles appear to be absent from the geologically older forms with distichous phyllotaxy, they are probably a later development of the more modified stems (32).

There seems no reason to assume a close affinity between such strikingly different forms as the Psaronieæ on the one hand and the Botryopterideæ, Hymenophyllaceæ and Gleicheniaceæ on the other.

In the Matonineæ we meet for the first time the polycycly so characteristic of most Psaronieæ. But *Matonia*, though polycyclic, is not dictyostelic. This fact, and the peculiar branching of its frond, appear to forbid a close affinity between the two orders.

Many of the older botanists believed the Psaronieæ and Cyatheaceæ to be closely allied. More recently this has generally been denied (42), (38). But Rudolph, who has recently reinvesti-gated the Psaronieæ very fully, would derive the Cyatheaceæ *b* them. He regards the recent Tree Ferns as a series showing *len* e reduction, this reduction being greatest in the simplest form *u r c*

even the most complex of existing Cyatheaceæ as having undergone, in their evolution from the Psaronieæ, simplication of the stele (32). Mr. Gwynne-Vaughan's researches, however, clearly show that the Cyatheaceæ form a series of increasing anatomical complexity, and that the more primitive solenostelic forms were almost certainly derived from protostelic ancestors (20). Among other differences between the two orders may be mentioned the diarchy of the Cyatheaceous roots and the polyarchy of those of the Psaronieæ.

Rudolph states that if we imagine the reduction suggested by him for the Cyatheaceæ to be continued we reach the vascular system of the Polypodiaceæ, and are faced by the possibility of joining them anatomically on to the Marattiaceæ. "It is, however," he adds, "naturally equally conceivable that the Polypodiaceæ are derived directly from forms with a simple axile strand, without having passed through a circuitous course of reduction from the Marattiaceæ" (32). Mr. Tansley's and Miss Lulham's interpretation of the *Lindsaya*-stele (44), and Mr. Gwynne-Vaughan's (20), and Mr. Chandler's (16) work on the Polypodiaceæ, however, clearly show that the latter alternative is the more acceptable, and that the Polypodiaceæ are, on the whole, a series of increasing complexity. These objections apply with equal force to a close affinity with *Loxsoma*; the latter being monocyclic differs more apparently from the Psaronieæ.

The anatomy and sequence of the fossil Osmundaceæ show that this order is very remote from the Psaronieæ. Further it is obvious that neither Marsileaceæ nor Salviniaceæ are at all closely related to the Psaronieæ.

MARATTIACEÆ.

The Marattiaceæ are dictyostelic; in *Archangiopteris* there is a circle of bundles, usually enclosing an internal strand, but the latter may be absent locally and the vascular system become temporarily monocyclic (21). *Kaulfussia* and *Danæa* are slightly more complex, for in them an internal strand is constantly present and rather better developed. *Marattia* may possess as many as three concentric series of bundles (11), while in *Angiopteris* there are numerous zones of anastomosing strands. There is every reason to suppose that the simpler genera are the more primitive, and that the series is one showing progressive elaboration of the stele.

In *Marattia* and *Angiopteris* a little secondary xylem and cortex is developed from a local irregular cambium. In *Angiopteris* the elements of the secondary wood are but half lignified (23). These

facts, and the circumstance that these phenomena are confined to the two anatomically most complex genera, suggest that the secondary tissues have been recently acquired.

Professor Bower regards the sorus of free sporangia, found in *Archangiopteris* and *Angiopteris*, as a modification of the synangial sorus found in the three other genera. The priority of one or other of these types is, as he asserts, not clearly proved; further, the older fronds with non-soral sporangia cannot, as he points out, be used as evidence of the phylogenetic development within the sorus itself (5). But against the primitiveness of the synangium among the Ferns it should be urged that the sporangia of some Pterido-sperms are more or less coherent, and as the latter are a relatively ancient group, some of the older synangia probably belonged to them. Mr. Kidston has shown that the cohesion of the sporangia in the Pteridosperms was probably secondary (27), and this favours the view that the common ancestor of Ferns and Pteridosperms possessed free sporangia, especially as the sporangia of the oldest *distinctly cryptogamic* fern-like plants, the Botryopterideæ, were typically (though not invariably) free. It has often been assumed that since some Psaronieæ bore Pecopterid fronds, and since some species of *Pecopteris* bore synangia, these synangia belonged to *Psaronius;* this supposition has been held to favour the primitiveness of the synangium in the Marattiaceæ. But as at least one *Pecopteris* was a Pteridosperm, and as its microsporangia are unknown, some or all of these synangia may belong to the Pteridospermeæ (18). As we are not certain that the fructifications of the Psaronieæ were synangial, or even that *Psaronius* was a fern, this argument is of little value.

But Professor Bower relies chiefly on the developmental evidence to show that the synangium is a sporangium multilocular by septation; if so, as the free sporangia of *Angiopteris* are clearly homologous with the loculi of the synangium of *Marattia*, the sorus with free sporangia is a derivative condition (5). In support of the hypothesis that the septa between the loculi are sterilized sporo-genous tissue, Professor Bower urges that though the archesporium usually arises from a single cell, yet a cell-packet outside the definitely fertile group may become sporogenous, or conversely certain cells usually sporogenous develop as tapetum. The latter case must be admitted to be an example of sterilization, such as occurs in the sporangia of many Pteridophyta. That the arche-sporium of each loculus is not always referable to the division of a single cell can hardly, however, be held to indicate that these loculi

arose by septation of a unilocular sporangium; for in the Lycopods the archesporium arises from a row of cells and additions seem to be made to it later (3). Yet among the Lycopods there can be no question of septation, since the sporangia are solitary. It would seem that in bulkier sporangia, such as those of the Equisetales and Lycopodiales, the archesporium arises from more than one cell. In *Ophioglossum* more than one cell still contributes to the formation of the archesporium (4). In the Marattiaceæ this contribution has, in accordance with the smaller size of the sporangia, become inconstant and irregular; in the leptosporangiate ferns, the sporangia of which are as a rule the smallest found among the Pteridophyta, the archesporium originates from a single cell. This is presumably due to their reduction in size.

Besides the fossil and developmental evidence, Professor Bower relies on an analogy with the anthers of certain Angiosperms that have clearly become multilocular by septation (4). He states that these show a close parallel to the details described for *Danæa*, and afford strong support of his theory that the synangium is a septate sporangium (5). But as he himself remarks, in a later paper, examples of fusion of sporangia also occur among the Angiosperms (7). In view of this fact and of the remoteness of the Angiosperms from the Marattiaceæ the analogy with the septate anthers should not be allowed to carry much weight. Thus, though it is not certain whether free or coherent sporangia are the more primitive, the evidence on the whole points to the priority of the sorus with free sporangia.

It seems absolutely useless to look for the nearer allies of the Marattiaceæ among orders so unlike them as the Botryopterideæ, Hymenophyllaceæ, Gleicheniaceæ or Schizæaceæ. The polycycly of the Matonineæ certainly recalls that of the Marattiaceæ, but it is associated with solenostely and almost certainly arose independently of the polycycly of the latter order.

The origin of the dictyostelic polycycly of the Cyatheaceæ and Polypodiaceæ may be traced within the limits of these orders, and as it is impossible to derive the Marattiaceæ directly from either of them, it is clear that the close similarities of the stelar structures are due to parallel development. Among the differences forbidding such a derivation may be mentioned the position of the protophloem (exarch in the Cyatheaceæ and Polypodiaceæ, endarch in the Marattiaceæ), the polyarchy of the roots of the Marattiaceæ, and the contrast afforded by the free annulate sporangia of the Tree Ferns and Polypodiaceæ, with their basipetal or mixed succession

on a receptacle, to the frequently coherent exannulate sporangia of the Marattiaceæ that always originate simultaneously. *Loxsoma* differs from the Marattiaceæ in the same ways as the Cyatheaceæ and Polypodiaceæ, and its stele affords none of the homoplastic similarities to the Marattiaceæ found in the polycyclic forms of both these orders.

Dr. Campbell remarks that the Osmundaceæ are undoubtedly intermediate between Eusporangiatæ and Leptosporangiatæ, but that it is difficult to say whether they come closer to the Ophio-glossaceæ or Marattiaceæ. He concludes that all these forms spring from one type, but that no two are directly related (13). Professor Bower also holds that in size, structure, and mode of origin of the sporangia, the Osmundaceæ are intermediate between the Lepto-sporangiate forms and the Marattiaceæ (6). The sub-eusporangiate origin of the sporangia of the Osmundaceæ may well be a primitive character retained by them and the Marattiaceæ from their common ancestor, for the small sporangia of the Leptosporangiatæ are the only Pteridophytic sporangia that originate from a single cell. It is hard to say whether the endarchy of the phloem in the Marattiaceæ and Osmundaceæ, unknown in other Ferns, is a primitive character, or whether it originated independently in the two orders. Mr. Gwynne-Vaughan's view that the two cases are not strictly comparable supports the latter alternative (21). In any case the geological history of the stele of the Osmundaceæ fully bears out Dr. Campbell's view that there is no direct connection between the latter order and the Marattiaceæ.

The Marattiaceæ show but few resemblances to the Salviniaceæ or Marsileaceæ, but to the Psaronieæ their likeness is curiously exact. The elongation of the steles of the Psaronieæ and the presence in them of purely cauline tracts of tissue are due to the fact that, unlike the Marattiaceæ, whose phyllotaxy is usually spiral, the leaves, and therefore the leaf-gaps separating the meristeles, are disposed in few more or less widely separated orthostichies. In the dorsiventral *Kaulfussia*, however, the leaves are confined to the dorsal part of the rhizome and the ventral part of the vascular system remains purely cauline. The "peripheral steles" of the Psaronieæ are absent from the Marattiaceæ, but as these do not occur in the older species of *Psaronius* with distichous phyllotaxy they are probably a later development of the more modified species. Rudolph's researches have done much towards re-establishing the comparison between the root-traversed cortices of the Psaronieæ and Marattiaceæ. Among other similarities between the two orders

we may note the polyarchy of their roots, rare among Ferns, and the fact that the Marattiaceous leaf-trace is a modification of the C-shaped type found in *Psaronius*. On the whole these resemblances suggest that the Marattiaceæ were derived from the Psaronieæ or their near allies, though, owing to the doubts that have arisen concerning the fructifications of *Psaronius*, this evidence is not so strong as it was thought to be. The ontogeny of the stele of the Marattiaceæ does not support the view that they are reduced from more complex forms, so that, if descended from the Psaronieæ, they probably arose from the simpler types.

OPHIOGLOSSACEÆ.

Only the Ophioglossaceæ remain to be considered. Of the three genera of this order *Helminthostachys* comes nearest to the hypothecated protostelic ancestor; its xylem is mesarch while that of the other genera is endarch. In them the whole of the centripetal xylem has been lost and replaced by pith and centrifugal wood, while in *Helminthostachys* this process is not complete. A further progression may be traced in *Helminthostachys*, *Botrychium* and *Ophioglossum*. In the first genus, xylem and phloem form a ring, broken only by leaf-gaps (13); in the second the xylem, though not the phloem, has become broken up into approximated strands, while in *Ophioglossum* xylem and phloem are broken up and associated in collateral bundles separated by wide medullary rays. But *Ophioglossum* always passes through an ontogenetic stage in which, as in *Helminthostachys*, xylem and phloem form a ring, broken only by leaf-gaps (24), and this stage may be retained by the mature rhizome of *O. Bergianum* (4). It would seem natural to regard the secondary growth in thickness of *Botrychium* as a recent acquisition, and its absence from the relatively simple *Helminthostachys* favours such a view, but the presence of a little secondary xylem in so small a form as *Ophioglossum vulgatum* is puzzling on this hypothesis.

The sporangia of this order are borne on one or more usually adaxial spikes, the nature of which has been much discussed. But as the spikes are clearly homologous throughout the order, the question is whether the forms with fewer and simpler spikes and fronds less often divided are more primitive than those with more highly compound fronds and more numerous and branched spikes. In *Ophioglossum vulgatum* and *O. pendulum* the lamina is normally unbranched and bears a single spike adaxially; in *O. palmatum* the compound lamina bears one to fourteen spikes. In *Botrychium* the adaxial spike is usually pinnately branched and may be three or

four times pinnate (4); but in *B. simplex* it is unbranched. In *Helminthostachys* the compound frond bears an irregularly branched adaxial spike. Those who, like Professor Bower (4) and Mr. Worsdell (45), homologize the spike with the Lycopod sporangium, and the subtending lamina with the sporophyll, naturally regard the simpler forms as primitive. Professor Bower, in his later publications admits the filicinean affinities of the gametophyte and makes of the order a phylum intermediate between the Ferns and the other Pteridophyta. Reasons for the inclusion of the Adder's Tongues in the ferns will be given in discussing the affinities of the phyla. Those who agree with Dr. Campbell that the spike represents the sporogonium of the Bryophyta, will probably also agree with him in regarding *Ophioglossum simplex* as the most primitive species, for in some cases at least it seems to possess a terminal spike devoid of a lamina (8), though in others a small blade is present (10). Dr. Campbell regards this species as the most primitive Pteridophyte, looking upon its spike as terminal and as representing a sporogonium, and its other organs as outgrowths from the spike (15), (13). The numerous and grave objections to such a view are bound up with the question of the origin of the Pteridophyta and lie outside the scope of this article. The fact that the sterile leaf of *O. pendulum* has no adaxial bundles, such as are found in the fertile leaf, even at the base of the petiole is, as Dr. Campbell claims, a strong reason for supposing that the spike, when present, really extends to the base of the petiole. But this does not prove the spike to be terminal and the lamina a lateral outgrowth from it; for it seems more natural to regard spike and lamina as branches of the frond. Dr. Campbell practically admits this alternative, for he says that if the spike be not regarded as terminal and the lamina as lateral it would seem natural to return to Mettenius' view that the leaf is divided into equal branches (15). The view that the spikes represent branches of the frond, though not always neces——— ———— sarily primary or equal branches, seems the most natural one. Iᵗ hostic is supported by the course of the vascular bundles of the fertile leaf ᵉ corof *O. pendulum* and of the complex *O. palmatum* (9), by the pinnati ᵗ of on of the spike of *Botrychium* and its irregular branching in *Helmi*ₐl snthostachys, and by the termination of the sporangiferous projection as .s of the spike of this genus as laminar expansions beyond the sporang. ʰia; these projections —the so-called sporangiophores—would then repre... ᵉnt pinnules. The forms in which a simple leaf bears a single spike wou... ld then be reduced, while the abnormal specimens of *Ophioglossum vulgatum*, figured by Professor Bower, would be reversions instead of progressive

elaborations (4). The substantial though inexact parallelism shown by this botanist to exist between the number of sterile lobes and of fertile spikes is equally compatible with a process of gradual reduction as with one of gradual elaboration; and though Professor Bower regards the simpler forms as the more primitive, yet in discussing the origin of the leaf-trace he admits, in a foot-note, that the simple *O. pendulum* and *O. simplex* belong to a section of the genus believed to be highly specialized (9). But it may be argued that the spikes are usually adaxial, marginal ones being rare (4). Against this it may be urged that the fronds of many Botryoptrideæ branched in more than one plane (40), and that branching into dorsal and ventral lobes occurs in the sterile leaf of *Azolla* and the fertile frond of the Marsileaceæ, though here the adaxial sporocarp is said to originate marginally (25), (26).

The gametophyte of the Ophioglossaceæ is subterranean, completely saprophytic and colourless (except in *Ophioglossum pedunculosum*), and more or less radially constructed. On typical dorsiventral fern-prothalli, the gametangia are on the lower surface, in *Helminthostachys* and *Ophioglossum* they occur all round the radial prothallus, while in species of *Botrychium* the somewhat flattened prothallus bears gametangia on its upper surface only (12), (30). This distribution of the gametangia suggests that the prothallus of *Botrychium*, instead of being intermediate between that of most Ophioglossaceæ and of other ferns, is a modification of the radial type, and is advantageous in that its gametangia probably arrest the water percolating the soil more easily and increase the probability of fertilization (30).

The Ophioglossaceæ show certain resemblances to the Botryopterideæ. In both, the wall of the sporangium is more than one cell thick and the frond frequently branches in more than one plane; in the Adder's Tongues, however, this branching in a dorsiventral plane is confined to the fertile fronds. Multiseriate pitted tracheæ occur in both orders and may well be primitive, for though rare in recent ferns they are characteristic of the Pteridosperms and these probably had a common origin with the Filicales from fern-like plants. Indications of the development of parenchyma at the centre of the stele occur in *Zygopteris corrugata*; an increase of this tendency might easily give rise to the stele of *Helminthostachys* (the most primitive in the Ophioglossaceæ) with its central pith and ring of wood. The Ophioglossaceæ seem to be vegetatively more reduced than the Botryopterideæ and the frequent dichotomy or dichotomous venation of their fronds is a primitive character showing that,

though their ancestors may have been closely allied to the Botryopteridæ, they cannot be descended from any known member of the latter order.

The Hymenophyllaceæ are clearly but distantly related to the Ophioglossaceæ.

Those species of *Schizæa* in which there is a woody ring surrounding a pith resemble *Helminthostachys*, but this similarity is obviously homoplastic, for the stele of *Schizæa* was clearly derived from a protostele within the limits of the Schizæaceæ. Briefly, though the Ophioglossaceæ show in their stelar structure and the frequent dichotomy or dichotomous venation of their fronds certain resemblances to the simpler Schizæaceæ, they differ strikingly from them in important points, such as the position of the sporangiferous part of the frond, the origin and structure of the sporangia, and, most important of all, the structure of the prothallus. The two orders do not, therefore, appear to be closely related.

The Gleicheniaceæ, Matonineæ, Cyatheaceæ, Polypodiaceæ and Loxsomaceæ differ even more obviously and widely from the Ophioglossaceæ.

In *Osmunda* we frequently find a ring of endarch xylem bundles, separated by medullary rays and surrounded by a ring of phloem; this recalls the structure of *Ophioglossum*, though here the phloem too is broken up, and is associated in collateral bundles with the xylem. In *Botrychium* and *Helminthostachys*, however, the phloem remains continuous. The mesarchy of the latter genus finds its counterpart in *Todea*. The study of fossil types shows that the Osmundaceæ are descended from protostelic forms and this is presumably true of the Ophioglossaceæ. The presence of internal phloem in some Osmundaceæ and a little secondary xylem in some Adder's Tongues is not an important difference, for these tissues are absent in the simpler members of the respective orders. In both orders we find multiseriate pitted tracheæ, which appear, on comparative grounds, to be primitive; further in both orders more than one cell contributes to the formation of the sporangium. These characters appear to indicate a certain affinity, but the essential difference between the radially symmetrical Ophioglossaceous prothallus and the dorsiventral one of *Osmunda* and *Todea*, and the scarcely less important difference that an adaxial sporangiferous branch of the frond is found in the one and not in the other order, renders a close affinity between them very unlikely.

The Marsileaceæ appear to be very remote from the Ophioglossaceæ; but it is interesting to note that in both the sporangia

occur on a more or less modified ventral lobe of the frond. The marginal origin of the sporocarp reported by Mr. Johnson, renders this likeness less exact.

To the Salviniaceæ and to the Psaronieæ (so far as we can judge from the vegetative organs of the latter with which alone we are acquainted) the Ophioglossaceæ show few indications of affinity.

Though the Marattiaceæ and Ophioglossaceæ are usually grouped together as the Filicineæ Eusporangiatæ, the connexion between them does not appear to be close. The eusporangiate origin and exannulate condition of the sporangia may well be primitive in both, but the different structure of the gametophyte and stele show that their ancestors must have begun to diverge from one another a very long time ago.

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NOTES ON RECENT LITERATURE.

PHYSIOLOGY.

THE LONGEVITY AND VITALITY OF SEEDS.

ONLY recently has there been made available any large body of trustworthy data upon the duration of viability in seeds. In 1907 P. Becquerel[1] published a valuable research upon the conditions which affect the vitality of seeds, and this includes tests of the viability of seeds of known and considerable age of some 500 species. In 1908 Ewart[2] published a similar list of tests made by him upon more than a thousand seeds in Australia, together with a collation of other such data collected from botanical literature.

We may consider first the data now available upon the longevity of seeds and then Becquerel's work upon the nature of the dormant vitality in seeds.

Becquerel tested the germination of all the oldest seeds of known age (25 to 135 years), preserved in the Natural History Museum of Paris. These represented 500 species belonging to 30 families, of which only 50 species produced seedlings, and these species were all included in four families; the majority in Leguminosæ, a few in Nelumbiaceæ, Malvaceæ and Labiatæ. The veteran seeds that germinated were as follows :—

[1] Becquerel. Recherches sur la vie latente des graines ; Ann. des Sci. Nat., Bot., Ser. IX., T. V., 1907, pp. 193-310.

[2] Ewart. On the Longevity of Seeds ; Proc. Roy. Soc. of Victoria, Vol. XXI., 1908, pp. 1-211.

Cassia bicapsularis; 87 years old, 3 out of 10.
Cytisus biflorus; 84 years old, 2 out of 10.
Stachys nepetaefolia; 77 years old, 1 out of 10.
Trifolium arvense; 68 years old, 2 out of 10.
Ervum Lens; 65 years old, 1 out of 10.
Lavatera pseudo-Olbia; 64 years old, 2 out of 10.
Nelumbium codophyllum; 56 years old, 4 out of 5.
Nelumbium asperifolium; 48 years old, 4 out of 5.

Becquerel was able to make a significant generalisation about the type of seed that shows such considerable longevity: he observed that in all cases these seeds had exceptionally strong and impermeable integuments.

Ewart's paper contains a list of over 4,000 cases. About 3,000 are his own observations (many are duplicates) and the rest (including Becquerel's) are drawn from botanical literature. The number of seeds tested in each case and the percentage of successes is always recorded by Ewart: this latter is probably a point of some significance. His own observations were made mostly on a store of seeds of 600 species which he discovered locked up in a cupboard in Melbourne, and which had been sent out from Kew in 1856 for a projected botanic garden in Melbourne, but never used.

Here again it was found that the Leguminosæ furnished more than half the number of cases of great longevity. In most of these the seeds are what is technically known as "hard" seeds, that is seeds which do not swell up when put in water.

In a number of species of Leguminosæ the seeds are provided with a particularly thick and resistant waterproof cuticle, and such seeds can only imbibe water when the continuity of this cuticle is broken. Becquerel took the precaution to break off a portion of the integument in his tests, and Ewart removed it by soaking the seeds for fifteen to ninety minutes in concentrated H_2SO_4 which is then neutralised and washed away, whereupon the seeds swell readily. As an appendix to Ewart's work Miss White verified the presence of this resistant cuticle by microscopic examination (drawings are given) and determined that the time of soaking in acid required was in proportion to its thickness. The seed of *Adansonia Gregorii* furnishes an extreme case and sometimes requires more than six hours in sulphuric acid to remove its cuticle.

The fact that seeds thus hermetically sealed show the greatest longevity suggests that protection from some external influence is a factor in the preservation of viability.

Becquerel established the further interesting point that not only are these "hard" integuments impervious to air, but that the dry testa of an ordinary pea or bean is also quite air-proof. He demonstrated this by fitting up detached pieces to close the top of the tube of a Torricellian vacuum, and he found that no air was sucked through the testa even in many months: the micropyle even is naturally hermetically sealed in some way and allows no air to pass. However, if the air in contact with the piece of testa is saturated with water vapour, then the testa slowly absorbs water and presently begins to allow air to pass by diffusion. As these phenomena hold with uncuticularised integuments it is concluded that pure cellulose walls are impervious to air when completely dried.

The tissues of the *embryo* of Leguminosæ were found by contrast to have a system of fine intercellular spaces and be quite porous so that air is readily sucked through a piece of the cotyledon of a pea or bean.

A really dry seed is thus isolated from gaseous exchange with its environment. " Air-dry " seeds in the condition in which they are usually stored contain, however, from five to fifteen per cent. of imbibed water, and their integuments may not be quite impervious to air. Seeds are indeed very hygroscopic and absorb water in proportion to the humidity of the air. Jodin[1] has recorded the varying weight of seeds in different meteorological conditions, and one of the few changing factors in an ordinary resting seed stored in air must be this alternate taking up and giving off of water. It has been suggested that the ceaseless slight molecular changes involved in this process slowly disorganise the viable protoplasm and in time cause the death of the seed. From such changes a " hard " seed would be exempt. It is therefore probable that complete dessication and preservation in a dry environment are necessary conditions for testing the maximum longevity for any plant whose seeds are among the majority in which the testa is not impermeable to water.

Extensive tests have not yet been made on these lines, but some have been started by Becquerel.

Complete dessication is a lengthy process which can be accomplished by maintaining the seeds for three months in a vacuum at 45°C in presence of caustic baryta. Hard seeds must have their testa perforated before they can be dried at all.

It has been maintained that seeds preserve their vitality longer if buried in natural damp soil, but it seems clear now that this is the exception and that most keep better dried (Duvel, U.S. Dept. of Agricult., Bull. 83, 1905).

There are a great many cases recorded in journals in which it is concluded that seeds must have been preserved alive for very long periods, perhaps many centuries, buried more or less deeply in the earth. Cases in point are the appearance of plants unknown in the district on the mud dredged from Poole Harbour and spread on the surrounding land (Salter, Journ. Linn. Soc., 1845); and a similar phenomenon on the Avon at Bristol (White, Trans. Brist. Naturalists' Soc.).

In a case recorded by von Heldreich the definite longevity of 1,500 years was claimed for the seeds of *Glaucium Serpieri*. This plant, then unknown in Greece, appeared in quantity when the heaps of refuse from the classical silver mines at Laurium were cleared away from the surface of the ground in the nineteenth century.

In such cases it is impossible that there should have been adequate supervision, and it will not do to attach credence to the extreme examples ; further it is found now by experiment that the plants recorded as appearing in most such cases have not hard seeds and shew no particular longevity—at least when preserved in air.

Another well known class of cases is the appearance of unaccustomed plants on the soil cleared by forest fires. Ewart has found hard seeds of *Acacia* spp. buried deeply in forests where there were no such trees within a mile, and he has also determined the

[1] Ann. agronomiques, T. XXIII.

numbers of buried germinable seeds at different depths beneath old forest Acacias. Thus beneath a tree of *A. dealbata,* per volume of eight cubic inches of soil, there were found twenty-eight seeds at a depth of three inches, sixteen seeds at nine inches, and three even at eighteen inches, all germinable.

Such provision of hard seeds accounts for some of the recorded phenomena ; but as Ewart points out the records of the occurrence of meadow seeds in the surface soil of forests rather than more deeply buried clearly point to efficient continuous distribution and not to longevity prolonged from before the period of afforestation.

In a final class of cases no credence at all is to be attached to sensational assertions of longevity. Here we find the alleged germination of wheat from Egyptian tombs and from the granaries of Herculaneum, etc. In genuine " mummy wheat " the embryo is always somewhat perished and has acquired a brownish colour, probably the result of slow oxidation.

We may now pass to some consideration of the fundamental question. What is the state of the protoplasm in dormant seeds ? Are vital processes going on continually though extremely slowly, or is all change at a standstill? In the time of Claude Bernard this was a burning question in Paris, and in 1861 a Committee of the Société de Biologie reported in favour of the latter view. This view was largely based on experiments in which seeds had been kept in ether, alcoholic corrosive sublimate, nitrogen, mercury, or a high vacuum for a year or two without loss of viability. These conditions involve suppression of any gaseous exchange of a respiratory nature, even when no active poison is present.

Other authors[1] have on the contrary asserted that ordinary dry seeds continually take in oxygen and give out CO_2, though of course to a very small degree.

Becquerel's recent researches have apparently harmonized and explained these contradictions by his discovery that the testa of most seeds is quite impervious at a certain degree of dessication. Now some observers have worked with seeds carefully dried and others with seeds in only their natural air-dry condition, when they still contain some 10% of water.

Obviously if the testa is dry and quite impermeable, then surrounding the seed with ether or alcoholic corrosive sublimate can cause no injury. Becquerel has shown that a perforation of the testa is all that is required to give a contrary result, and that once these noxious substances penetrate to the embryo the seed is killed.[2]

All that former experiments prove is that seeds can exist for a considerable time without any gaseous exchange with the environment. This might still be possible on a theory of immensely retarded vitality in which a minute, but continuous conversion of the oxygen contained within the testa into carbon dioxide was taking place.

To remove this possibility seeds were perforated and then dried completely and kept for two years in a high vacuum. Here there

[1] Van Tieghem et Bonnier; Ann. agronom., 1880, and Bull. Soc. bot. de France, 1882.

[2] In some seeds, *e.g.* Ricinus, the testa is fairly pervious, even when quite dry, and such are killed by ether, etc. even when the testa is intact.

was no loss of power of germination and we are reduced to thinking that if there is any respiratory change going on, then each cell must be living on its own supplies, for each cell-wall by dessication has become quite air-tight. Life may here fairly be described as anaerobic.

If these dry cells in vacuo have really entered into a quiescent state in which no change whatever is taking place—the state of "static equilibrium" as opposed to the "dynamic equilibrium" of the living ever-changing cell, then they should be capable of retaining their viability indefinitely. Time alone can settle this question and Becquerel has formally deposited seeds thus prepared in vacuo with the Bureau of Standards in Paris, and these are to be tested every ten years. Should they show no mortality, it is brilliantly suggested that then in this way standard plants may be handed down to remote posterity for comparison with the forms that evolution has produced in many generations of descendants!

Till then, it is said, the question between these two theories must remain in abeyance. The reviewer would point out that in theory, gaseous exchange with the environment is not essential for an energy-liberating "respiratory" change within the cell. In the respiration of anaerobes no oxygen is taken in, while in the respiration of succulents no carbon dioxide is given out. We could imagine a combination of these attributes in such a change as the slow conversion of sugar into lactic acid $C_6H_{12}O_6 = 2\ C_3H_6O_3$ by which a small steady supply of energy could be set free. Examination of the alteration of the cell-contents in seeds of great antiquity might give some clue.[1]

Becquerel's final contribution to the elucidation of the discordant results of previous workers is to show that whereas quite dry seeds have no gaseous exchange, seeds that are merely air-dry, may conduct a continual, though slight conversion of oxygen into carbon dioxide.

This is apparently a purely chemical oxidation, for, unlike respiration, it is increased by exposure to light, in particular blue light. Many carbohydrates are known to be slowly oxidised in sunlight in this way. Further Becquerel has shown that this oxidation is chiefly located in the testa, which when isolated, may alone account for as much CO_2 as the whole intact seed previously.

Such chemical oxidation of the substances in the cells of the resting embryo might, in time, destroy the organisation needed to maintain viability, even if the organisation were, as regards vitality, in a state of static equilibrium all along. If this is so, then it is essential that critical tests on the longevity of seeds should be performed in the absence of oxygen as well as of water, which, indeed, is provided for in Becquerel's standard experiments in vacuo.

There is one line of experimentation in this field in which all workers have got concordant results. All are agreed that the vitality of ordinary dry seeds is quite unaffected by exposure to extreme cold such as that of liquid air (—190°C) or that of liquid hydrogen (—250°C).

[1] At present there seem to be only the observations by Acton, (Ann. Bot., Vol. VII., 1893) that old perished wheat contained more soluble constituents and less water than viable grains.

It is generally stated that all chemical change must necessarily be in abeyance at such temperatures, and that therefore the seed cannot be in any other than a state of static equilibrium. A few chemical changes, however, still take place at these low temperatures, such as the union of hydrogen and fluorine, so that it is not philosophical to say that absolutely no change can take place in the cell. We need only recall the modern conception of the nature of the general relations between temperature and chemical change. According to this the rate of change will be lowered by some constant fraction for every 10°C fall of temperature. Therefore, however low the temperature, the change will only be indefinitely retarded, not absolutely stopped. It may well be that there will not be enough CO_2 produced to be detectable in a ten years, but who shall say that change has *ceased*. Our methods of analysis, which demand a large aggregate of molecules for any demonstration, are incapable of settling this philosophical question. We can only set up an arbitrary quantitative standard of a minimum, and agree to ignore all amounts below this.

Similar must be the relation between dryness of the seed and the rate of respiratory or other chemical change in the cell. There is no doubt that the rate of change falls off rapidly as dessication proceeds. Kolkwitz has shown that at summer temperatures one kilogram of Barley produced per 24 hours 3·59 mg. of CO_2 when it contained 19·2% of water, 1·4 mg. when it contained 14% of water, and 0·35 mg. when it contained 11% of water. This curve might be extended, when it will continually approach the value of zero, but at no degree of dessication will the change theoretically cease.

It is not even as if we could *absolutely* dry our seed; we can only go on till it is in equilibrium with the particular drying agent used: there is no finality in such procedure.

Philosophically then we reach the conclusion that neither cold nor dessication is capable of distinguishing experimentally between the two hypotheses as to the nature of the latent vitality of seeds. Experimental tests based upon the power of resisting extreme high temperatures are not open to this critical objection, but this leads us beyond the scope of the present review.

F.F.B.
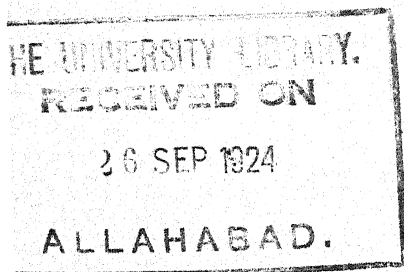
HYDRODYNAMIC FACTORS INFLUENCING PLANT-LIFE ON SANDY SEA SHORES.

By PEHR OLSSON-SEFFER, PH.D.,

Mexico City.

IN a recent paper[1] I have used the expression hydrodynamic factor to signify the influence of water in the soil upon plant-life as distinct from edaphic and atmospheric influences. The water-content of the substratum is recognized as one of the most potent factors in plant-life, and in the study of vegetation on sand-formations and the conditions there existing, the peculiar relations of sand to the water contained in the soil will at once force themselves upon the observer.

Sand, of all natural uncultivated soils, ranks highest in porosity, and lowest in capacity of retaining water, and, as is well known, it is the retentive power of a soil which determines its suitability to a certain kind of vegetation. It is the volume of water a soil is capable of placing at the disposal of the plants, which is the limiting factor in production of its vegetative covering and the controlling condition in the distribution of this vegetation. And it is not only as a factor in the growth of plants that water-content of the soil is important. In the case of sand, which under certain conditions is liable to drift, the soil-moisture is of the greatest consequence in checking this movement. Taking perfectly dry, pure quartz sand as zero, a mixture of only 4% of water gives it so much coherence that it may be pressed to a ball in the hand, and cease to be driven by the wind.

PERCOLATION OF WATER.

But on account of its peculiar properties, sand allows the precipitation to percolate rapidly, and the acting force, gravi-

[1] Pehr Olsson-Seffer. " Relation of soil and vegetation on sandy sea shores." Botanical Gazette, Chicago (in the press).

tation, is so effective that except for the counteracting influence of surface-tension very little water would be retained in the sand. The permeability of sand is variable according to the texture of the soil, and it increases as the particles increase in size. Lysimetrical measurements given by Wiley[1] show that in ten hours' time under a water-pressure of 10 cm., 0·151 liters will pass through a layer of sand 10 cm. thick of 0·01—0·71 mm. grain-diameter, while with a water-pressure of 100 cm., 0·596 liters will percolate through the same sand 10 cm. deep in the same time. With a sand of a coarseness of 0·071—0·114 mm. the corresponding amounts of water filtrated are 2·194 and 8·530 liters.

Comparing sand with soil of finer texture we find that the greater permeability of the former depends on the fact that the interspaces between the soil-particles are so large that they are not filled with the fine sediment which is brought down from the surface with the sinking water, while in the case of clay its almost complete imperviousness is due to the *inability of the soil-air to escape upwards through the super-saturated surface.* So long as this air cannot escape it prevents the water from entering the soil-spaces occupied by it (King). In fine sand the water therefore does not sink so rapidly as in coarser, and it can be observed after a heavy rain that on those places on a dune where the finer material is accumulated, the water has not penetrated so deep as where coarser grains compose the bulk of the sand. The air has been confined under the water, and impedes percolation until an escape is affected either upward or laterally. This circumstance makes it difficult to use cylinders or vessels with closed sides for experiments on the downward movement of water, and by allowing the air to escape laterally the source of error will always be considerable. The values obtained by such experiments are therefore relative, and cannot be compared unless the experiments are conducted under conditions as nearly similar as possible. I have made a number of attempts to determine the relative rate of percolation in sands of different coarseness, but the results have not satisfied me as being a true index of the power of filtration, because of the difficulties in establishing conditions approximately similar to those in nature. I do not therefore feel justified in mentioning the results obtained, and I must add that in the case of all the data I have seen in the literature, those quoted above included, we have to accept them with

[1] Principles and practice of agricultural analysis, 1895, Vol. I., p. 163.

the reservation indicated. The artificial conditions under which measurements of the rate of percolation are usually conducted, whether it be after the methods of Deherain, Whitney, Welitschowsky or others, make it important that in giving the results the details of the method should be furnished.

To obtain the absolute value of the rate of percolation is hardly possible, as we cannot control the lateral translocation, which depends largely on the topography of the surface, a circumstance which is rarely taken into consideration in the various devices for determination of the power of the soil for permitting the downward flow of water.

Seelheim[1] has given the following general laws for the rate of percolation, based on a great number of careful experiments.

The quantity of water passed through the sand is :—

    (1)   proportional to the pressure ;

    (2)   inversely proportional to the thickness of the layer ;

    (3)   proportional to the area of the layer ;

    (4)   proportional to the square of the radius of the sand grains ;

and with increase in temperature the rate of percolation increases.

The Water-Content of the Soil.

Only a few decimeters below the surface sand-formations are always moist, even on the top of the highest dunes. To account for this remarkable fact it was long assumed, and is still held by some observers, that the acting force was the capillarity. Andresen has doubted this, and he maintained that the humidity can be explained only by evaporation from below. He states the mean minimum of water contained by the sand of the dunes of Jutland, 0·3 m. below the surface after a long drought, at 2 per cent., and the maximum after a rainy month at 4 per cent. At greater depth the quantity is larger.[2] The hygroscopicity of the sand of the coast of Jutland he found to be 33 per cent. by measure, or 21·5 per cent. by weight. The annual precipitation on that coast is 27 inches, and as the evaporation is about the same, he argues that rainwater does not penetrate far beneath the surface of the dunes.

Before proceeding to my own observations in this matter, some interesting data by Kerner[3] will be referred to. He found that the

[1] Die Durchlässigkeit des Bodens für Wasser. Forsch. a. d. Geb. d. Agric.-Physik. Bd. 3, 1880.

[2] Andresen : (l.c., p. 106).

[3] Die Aufforstung des ungarischen Tieflandes. Monatsschr. f. Forstwesen, 1865.

sand, during dry periods or a few days after rain, was moist three to four inches below the surface in spring, six to seven inches deep in summer and two to three inches in fall. "Ein solcher Sand," he says, "den ich in regenloser Zeit im Monat Juli in einem der ödesten Flugsandreviere aus der Tiefe von 1 Schuh schopfte, und den ich zur Vermeidung der Verdunstung rasch in ein luftdicht verschliessbares Gefäss fullte, zeigte bei nachträglicher Erwärmung auf 100°C einen Gewichtsverlust, aus welchem ich einen Wassergehalt von 4·065% berechnete."

Kerner's experiments to ascertain the hygroscopicity of sand gave the following results : during twenty-four hours a sand of 1/20 line grain-size absorbed from the atmosphere, saturated with moisture, 1·78%, another sample of 1/15 line grain-size, 0·78%, and a still coarser sand, 1/10 line, only 0·42%. The evaporation of moisture he found to be greater the coarser the sand. During twenty-four hours the first sample lost 76·1%, the second 85·4%, and the third 96·4% of moisture.

Although determinations of capillary attraction in sand have frequently been made, the writer, wishing to obtain comparative data for the different degrees of coarseness of sand which have been considered throughout this study, conducted some experiments for this purpose in Maryborough, Queensland, in 1901. Eight glass tubes, filled with sand, 82 cm. long, 2·5 cm. internal diameter, were used, the lower end covered with fine brass netting, and sunk to 3 cm. in slowly running water of constant height. The following table gives the results obtained :—

No. of Sample.		1	2	3	4	5	6	7	8
Diameter of grains in mm.		0·03 0·05	0·05 0·1	0·1 0·2	0·2 0·3	0·3 0·5	0·5 1	1·2	2·4
Heights (in millimeters) to which water had risen in given times from beginning of experiment.	5 min.	21	20	18	17	16	12	10	8
	10 „	36	32	29	24	21	20	19	16
	30 „	73	63	57	54	48	33	22	17
	1 hour	87	84	83	80	62	42	25	18
	12 „	141	112	96	87	78	52	31	21
	1 day	174	137	113	99	84	60	32	22
	2 „	195	144	129	112	89	63	35	23
	3 „	212	160	141	123	93	66	37	24
	4 „	236	181	156	138	96	69	39	25
	5 „	250	196	164	149	100	73	41	26
	6 „	258	213	172	158	105	76	43	27
	1 week	265	220	189	162	112	80	45	29
	2 „	294	231	203	178	136	91	47	31
	3 „	321	257	215	190	154	100	49	33
	4 „	339	269	224	201	171	106	51	35
	8 „	382	297	243	229	188	111	54	37

The sand used for these samples was almost pure quartz sand, completely dried before placed in the tubes. The results show that in finer sand, water rises much more rapidly than in coarser, and to a considerably greater height. A tube filled with clay was employed to ascertain the rate of capillary action in that soil, for comparison, but through an accident this tube was broken during the third week of the period. Enough was seen, however, to make it clear that while the rise in all the sand-samples was comparatively rapid during the first ten minutes after submersion in water, it was nearly four times slower in the clay. After a week's time the rate of rise in the clay increased in comparison with that of sand, and continued to do so.

The above results, which support those of Klenze, so often referred to by writers on the physical properties of dune sand, indicate that the rise of water by mere capillary action is slow, and, moreover, does not reach any considerable height.

In order to investigate this question still further, I had a well dug at the foot of a sand-dune near Perth, in Western Australia, for the purpose of establishing the level of the ground-water. The site of the well was 97 meters from the high-water mark of the ocean, and the water in the well stood at average low tide 23 cm. above the level of the sea. Minute observations were made of the fluctuations of the ground-water-level, which was found to be influenced by atmospheric conditions and by tidal oscillations.

Simultaneously measurements were taken of the rate of evaporation from the surface of the dune. This latter was 8·72 meters high above the water-level in the well, and thus 8·95 meters above sea-level. The well was 4·3 meters distant from the middle of the base of the dune.

The amount of rainfall during the five months covering the period of observation was 2·17 cm. It was found that a perceptible amount of moisture existed at 5·8 m. above the ground-water-level in the interior of the dune, but above this height, up to 7·4 m., the amount of soil-moisture was very small. The moisture then increased gradually, until it reached a maximum at 68 cm. from the surface. Again it decreased towards the surface of the dune.

In trying to explain this condition of the moisture-content in the sandy soil of the coastal dune, it should first be borne in mind that there is a general tendency of the ground-water to stand at the highest level under the highest ground. The second point is the capillarity, which considerably assists in raising the water, as the above mentioned experiments show.

The surface cultivation which obtains in the so-called "dry-farming" process results in a loose open texture of the soil for two to four inches, which very materially influences the capillary movements of the soil-moisture.

A similar result is noticeable in sand-formations where the sand is shifting.

Further, the third point to be observed is the surface tension of the water. Whitney has discussed this in several bulletins[1], and King[2] has experimentally proved many important questions in this connection.

The general principles under which this factor acts may be summed up as follows:—

1. Surface tension moves the water in any direction according to circumstances.

2. When water is removed from the soil by evaporation or by plants, surface tension attracts more water to the spot.

3. When rain falls on a dry soil, surface tension, together with gravitation, draws the water downward, even when gravitation alone would not be sufficient for that purpose.

4. Surface tension of water is increased by salts, while it is lowered by organic matters.

5. As the soil becomes drier the surface tension of the soil moisture is reduced.

6. Surface tension of soil moisture is much lower than that of pure water.

7. A soaking rain therefore increases the surface tension of the soil-moisture in the upper layers of the soil, and water is consequently drawn up from below. If excessive evaporation takes place immediately after the rain, not only the precipitated but also some of the water drawn from below may evaporate, and the soil is consequently left drier than it was before the rain.

It is known that the capillary movement of moisture is greater in moist sand than in dry, as has been demonstrated by many experimenters, and that it takes place much more rapidly and rises to a greater height than the capillary rise of moisture in dry sand. But the combined action of the three factors mentioned and the

[1] Some physical properties of soils in their relation to moisture. U.S. Dept. Agr., Div. Soils, Bull. 4, 1892.
Milton Whitney and Ralph S. Hosmer; Soil moisture. U.S. Dept. Agr., Div. Soils, Bull. 9, 1897.

[2] Observations and experiments on the fluctuations in the level and rate of movement of ground-water. U.S. Dept. Agr., Weath. Bur., Bull. 5, 1892.

conservation of the moisture which has fallen as rain, seem not to explain in a satisfactory manner the phenomenon of permanent moisture a little below the surface of high dunes, which is noticed also in deserts, where no rain has fallen, perhaps for years.

A more likely interpretation of this fact can be found in *internal dew formation in the soil.* In the layer above the ground water, the air which is present between the grains is saturated with moisture, and the absolute humidity of this soil-air corresponds to the yearly mean temperature of the layer of soil. At a depth of 60m. this temperature is only about two degrees higher than the mean temperature of the surface atmosphere. Now it is known that the saturation deficit with the same absolute humidity increases with the temperature. Through diffusion the air in the higher layers of the sand also tends to be saturated, and any lowering of the temperature diminishes the saturation deficit, until a temperature is reached when condensation of water vapour takes place.

While the small gradient in the mean annual temperature referred to does not seem to be sufficient to cause a deposition of moisture in the interior of the dune, it must be remembered that the diurnal and nocturnal temperature variations are considerable on an open sand formation, on which the radiation factor is one of considerable moment. Such fluctuations in soil temperature are periodical and are sufficient to cause periodical condensation of water vapour in the soil. While it is inconceivable that the apparently permanent moisture in dunes is due to capillarity alone, all the foregoing facts are in accord with the theory that the formation of dew in the soil is an additional cause of this moisture.

The adjustment of soil moisture to the varying conditions of the soil is largely regulated by the amount of evaporation. It will be noticed on dunes that they are often dry on the surface only a few hours after heavy rain. The drier the sand the more slowly percolation takes place, because of the difficulty in overcoming the repulsion offered by the dry grain. In fact, during a hot summer-day, when the surface is overheated, it will be found that a precipitation amounting to 1 cm. has not penetrated deeper than 70 mm. To some extent this is due to an evaporation of the water caused by the hot grains. But if a low temperature has prevailed for some time, even if the sand previously has been quite dry, the water percolates to a much greater depth, because in this case the lower temperature no doubt had caused condensation of the water vapour

present in the soil air, thus increasing the amount of hygroscopic water, and bringing about to some depth a continuity which assists in a more rapid establishing of equilbrium.

Here we must not overlook the influence of changes in temperature on the coefficient of viscosity, which is known to decrease with higher temperature, and which largely determines the rate of flow of the water, as certain experiments by King[1] indicate. He found that—

At 9·01°C the flow was 6·153 grams per minute.

„ 9·23	„	6·27	„
„ 9·38	„	6·384	„
„ 12·6	„	7.046	„
„ 23·8	„	9·014	„
„ 32·46	„	10·554	„

These experiments refer to a saturated soil, and although other factors have to be taken into consideration in regard to the rate of movement of water in a soil, in which saturation is not complete, it remains without doubt that temperature changes, both diurnal and seasonal oscillations, greatly affect the rate of adjustment of soil moisture.

EFFECTS OF SALTS ON MOVEMENT OF SOIL WATER.

The above statement (4) (p. 42) in relation to the effect on surface tension by salts, is of some importance in a discussion of the hydrodynamic factors on coastal sands. It is well-known that the atmosphere on the seacoast has a certain percentage of salinity, and that this salt, under certain circumstances, is deposited, even in crystallized form, on the ground and on objects on the shore.

Whitney[2] gives the surface tension of a solution of common salt, of a specific gravity of 1·1, as 7·911 gram-meters per square meter, that is on a square meter of liquid surface there is sufficient energy to raise so many grams to the height of one meter. The corresponding surface tension of pure water was 7·532. This difference indicates that on coastal sands, where salt is frequently deposited on the surface, the tension must be increased and consequently water drawn from below. In agricultural practice it is also well known that application of salts tends to keep the soil more moist during dry weather. We can therefore assume as certain that on coastal sands the amount of moisture in the surface soil is larger than on inland sand formations, and this helps considerably in replacing the water that has evaporated or been used by the vegetation.

[1] U.S. Weather Bur. Bull. 5, 1892, p. 66.
[2] Ibidem 4, 1892, p. 16,

EVAPORATION OF MOISTURE.

Sand, as mentioned above, ranks lowest in water-holding capacity among soils, and this fact is due, to a great extent, to the facility with which evaporation takes place from a sandy surface. Kerner's observations, already referred to, make it evident that the coarser the sand the greater the rate of evaporation. The principal factors regulating this evaporation are :—

      (1) the temperature of the evaporating fluid.

      (2) the temperature of the atmosphere.

      (3) the wind, and

      (4) the degree of humidity in the air.

The rate of evaporation is :—

      (1) proportional to the evaporating surface.

      (2) proportional to the difference between the highest pressure of vapour at saturation and the pressure prevailing at the moment, and

      (3) inversely proportional to the atmospheric pressure.

A loose and open soil, such as sand, leaves the capillary tubes open to the surface, and evaporation therefore can proceed from them so freely that the underground store of moisture may be insufficient to supply the continuous demand of the vegetation covering. It is somewhat moderated by the amount of mould which acts as soil mulch, but as we have shown, the fine humus particles deposited on the sandy surface are rapidly carried downward into the ground with the percolating rain, when wind has not already taken hold of them, and transported them far away, and sand therefore contains very little humus.

Sometimes the evaporation of moisture from the leaves goes on more rapidly than the roots take up fresh supplies from the soil. This can often be seen on hot sunny afternoons in the latter part of the summer when the leaves are all limp and drooping. As evening approaches and the sun's evaporative power lessens, the supply of water from the soil again equals the demand of the leaves, and the latter assume their crisp character because the tissues become turgid with water.

The changes in evaporation which necessarily follow the changes in atmospheric humidity and pressure, vary with the diurnal oscillations of temperature, and are especially great on the sea coast. Sufficient data are not yet at hand to discuss in detail this matter of the march of evaporation on coastal sands, but enough is known to make it clear that greatly varying conditions

obtain in different climates and that especially local topography is of great moment. The coastal sand-formations have usually an open vegetation for some distance from shore, when forest follows, and the neighbourhood of the woods affects to some extent the rate of evaporation.

The influence of topography on evaporation can be noticed in the difference in vegetation on exposed places on the dunes, in the depressions and on the leeward side. Series of measurements of the rate of evaporation on coastal sands would be of considerable interest. The same objection that was expressed above regarding the mode of making meteorological observations in connection with ecological investigations holds good also in this case. The evaporimeters used need to be all alike, and the environmental conditions have to be carefully considered if the measurements are to be at all comparable. Relative values, which are sufficient for general climatological purposes are not satisfactory when we endeavour to interpret the ecological adaptations in the light of local meteorological conditions. We must attempt to get data representing as nearly as possible the absolute values.

THE EFFECTS OF THE SEA ITSELF.

The hydrodynamic factors which present themselves in the sea are necessarily of great moment to the adjoining shore formations, not only directly but also indirectly. On the submerged beach the seawater is the surrounding medium in which the vegetation lives, and all the physical properties of this medium are of the greatest consequence to the plants. Furthermore, wave action and currents in the water are here important factors influencing the plant-life. On the front beach most of these factors determine the conditions for the vegetation, while on the formations more distant from the water the influence of the sea is of a more indirect nature.

Action of Waves. There is a considerable difference in the influence of waves on shores with a steep, and with a gentle slope. The on-shore action of waves on a beach of gentle slope is of greater efficiency in working the sand landwards than on a steep slope. The undertow on the former shore is more interrupted by the breakers than where the shore is steep and the water deeper. Generally the agitation of the water on a shallow bottom is greater. The plants growing in places exposed to the full force of the on-rushing breakers must also necessarily be endowed with special appliances to be able to withstand the continuous wear and tear of the surf. Some of these adaptations will be mentioned later.

On many shores, which are protected by outlying banks or islands, the action of waves is considerably lessened, or, in some cases is absent. Such shores in different positions can be seen in abundance in the Archipelagos of the Baltic, while most other coasts observed by the writer in this connection have been unprotected from the open sea.

Except in their landward urging of sediments the waves are also incidental agents of breaking off and transporting fragments of plants both on the submerged and front beach.

Currents in the sea are, however, of still more marked significance for transportation of spores, seeds, fruits and shoots of plants, and must be considered as an important factor in the distribution of coastal floras.

To the plants living in the water, currents are of the greatest consequence because they continuously change the surrounding medium, thus bringing within reach of the plant the necessary foodstuffs. While some plants are able to exist in the heaviest surf, *e.g.*, many algæ and *Phyllospadix*, others prefer water with a steady current, and others again grow only in quiet water.

Salinity of sea water is another factor which exerts a great influence on those plants which come into direct contact with the water, and indirectly also on the shore vegetation by affecting the salinity of the atmospheric moisture. Most of the salts contained in sea water do not constitute any food for the plants, but are important by their influence on the turgor. It is, however, the variations and changes in the salinity on a given coast, which determine the aspect of the vegetation, rather than the larger or smaller amount of salts contained in the water. This is noticeable on many coasts where the salinity is stable, and not subjected to occasional diminutions by the influx of freshwater from the overflow of rivers. The general character of the sea-shore vegetation on the open coasts along the Baltic, with a salinity less than 1%, is similar to that of the North Sea shores with a salt-content in the water of 1·5% and of the West Coast of France with a salinity of 2·5% in the Atlantic Ocean. The sea coast of California presents a vegetation on the sands which does not materially differ from that of the Baltic, and even the sub-tropical coasts of Queensland, where the salinity is 2·9% show a closer relationship to the general marine coast vegetation of Europe, than do the sea-shore plants in the outer Finnish Archipelago to those in the innermost part of the same Archipelago, only about 200 km. distant, but with a salinity

that often changes through a large amount of freshwater being brought down by the rivers, and then for some time floating on the surface of the usual sea water, which contains a greater percentage of salts and consequently is heavier.

The rapidity with which a change in salinity takes place is further of the greatest importance for those plants which occur on the submerged beach. Many algæ which, as a rule, are able to live in salt water of the most extreme degrees of salinity, cannot bear a rapid change in this amount of salt, because of the considerable change in osmotic pressure which results in the cells.

Temperature of sea water. This factor is of some importance for the distribution of sand strand plants. In northerly latitudes, especially in some parts of the Baltic, where the water is liable to be converted into ice during winter, the vegetation on the submerged beach is very scanty, the plants are low and of a poor stunted growth.

The temperature of the sea water also to some extent influences the atmospheric temperature on the coastal sand formations. The writer's observations of the temperature of the sea water have been confined to the Baltic and to the coast of South Queensland.

In the Baltic, especially in the northern part, great variations in the temperature of the water occur. These changes are caused partly by the varying direction of the winds, or correspond to the seasons. During summer the surface water is often heated considerably, sometimes to 16^0 C. in the open sea, or $20\text{-}22^0$ C. in sheltered inlets, while in winter ice formation takes place. Continuous land winds often cause a fall of the temperature by driving seawards the warm surface water, which is then replaced by cold water. This is especially evident on steep, open shores.

Solar radiation greatly affects the temperature of sea water. In sheltered bays its influence is greater than on the open sea. An observation by the author, described in another place,[1] showed that while the temperature of the sea water in a small inlet in the Finnish Archipelago was $20 \cdot 6^0$ C. in the early morning with an atmospheric temperature of 23^0 C. and a salinity of $0 \cdot 521\%$, it had increased in six hours, during which time the solar radiation was intense, to 24^0 C. During the same period the atmospheric temperature had risen to 29^0 and the percentage of salt to $0 \cdot 564$.

As a rule, the surface temperature of the water is higher than

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[1] Några iakttagelser öfver hafsvattnets salthalt i Finska Skärgärd-shafvet. Geogr. För. Tidskr., XI., p. 262, 1899.

that of the atmospheric strata immediately above during fall and winter, and a considerable amount of heat is at that time absorbed by the air.

On tropical and sub-tropical coasts the variations in temperature of sea water are mainly due to change in the direction of wind and to currents. A series of observations made in 1901 on the east coast of Australia, near Brisbane, gave the mean temperature of the surface water during January, that is the hottest month of the southern hemisphere, as $22 \cdot 4^{0}$ C., in February $21 \cdot 1^{0}$ C., in March $20 \cdot 6^{0}$ C., and in April $19 \cdot 2^{0}$ C. The mean atmospheric temperature during the same periods was respectively $27 \cdot 2$, $25 \cdot 4$, $24 \cdot 3$, and $21 \cdot 6^{0}$ C. The highest daily variation observed was from $20 \cdot 6^{0}$C. at 8 a.m. to $23 \cdot 5^{0}$ at 6 p.m. on February 11th, with a corresponding change of atmospheric temperature from $29 \cdot 2$ to $32 \cdot 1$. After a prolonged period of continuous westerly winds, the temperature of the surface water fell three degrees, while it always rose after northerly and fell after southerly winds, the former bringing warm water from the tropics and the latter cold water from the south. Close to the shore or where the water is shallow, the temperature of the water is higher when the surface is calm, but low where the sea is rough. This is the natural consequence of the solar radiation in the former case, and of the mixing by the waves of the surface water with the colder water from below when the sea is disturbed.

The observations upon which the present paper is founded were made during a period of years on many sea-shores in Europe, Asia, Australia, South Sea Islands and North and Central America. Special attention was paid to the coasts of the Baltic and the east and west coasts of Australia. A dune district near San Francisco in California was studied in detail.

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THE PHYLOGENY AND INTER-RELATIONSHIPS OF THE PTERIDOPHYTA.

By Lady Isabel Browne.

VII.—THE INTER-RELATIONSHIPS OF THE PHYLA.

In discussing the affinities of the phyla it will be convenient to consider first the affinities of the Lycopod and then of the Fern phylum to the rest of the Pteridophytes, since these two phyla are curiously isolated. It is, as Mr. Tansley has recently pointed out, very difficult to suppose that any of the phyla originated independently of the others from widely separated ancestors, for in that case the roots and vascular tissues (including sieve-tubes and xylem) of such a phylum would not be homologous with the essentially similar structures of other Vascular Cryptogams (40). Nevertheless, Dr. Campbell regards the Lycopod prothallus as having originated independently of that of the Ferns and Horsetails from a very different type (12). The essential similarity of the gametangia throughout the Pteridophyta renders this very unlikely. The radial symmetry of the Lycopod prothallus certainly affords a striking contrast to the dorsiventral symmetry of the gametophyte of the Filicales and Equisetales. The prothallus of the Club Mosses has been compared to the radially symmetrical gametophyte of the

Adder's Tongues; but Dr. Lang has shown that the symmetry of the Ophioglossaceous prothallus is probably not primitive but an adaptation to a subterranean habit and that it may be to a certain extent induced in dorsiventral prothalli (26). The subterranean habit may have caused the radial symmetry of the prothallus of *Lycopodium*, for the most primitive type of prothallus found in the genus—that of *L. cernuum*—is less completely subterranean than the other types (except the highly modified type of *L. Phlegmaria*) and forms flattened expansions on reaching the light. Dr. Lang has provisionally referred a prothallus essentially similar to that of *L. cernuum* to *Psilotum* (27). Unfortunately some doubt rests on its attribution; otherwise it would be evidence in favour of a closer affinity between the Club Mosses and Psilotales than is now usually admitted, and might serve to bring the Club Mosses indirectly into connection with those probable allies of the Psilotales, the Sphenophyllales, and through them with the Equisetales. Great importance has been attached to the biciliate spermatozoids of the Lycopodiaceæ and Selaginellaceæ, which are unknown in Ferns or Horsetails. Those of *Isoëtes* are, however, multiciliate, and if the Lepidodendraceous descent of *Isoëtes* should be confirmed (it has been strengthened quite recently by the discovery of a Mesozoic fossil provisionally referred to the Isoëtaceous cycle of affinity (30)) there would be a *prima facie* probability that in this phylum also the spermatozoids were multiciliate.

Still less is it easy to agree with Dr. Campbell's view that the sporophytes of Ferns, Horsetails and Club Mosses originated independently from non-vascular forms. The discovery of *Protocalamites (Calamites) pettycurensis* shows that in the Equisetales, as in the allied Sphenophyllales, and in the Psilotales and Lycopodiales the centre of the axis was primitively occupied by centripetal wood. On comparative grounds it seems likely that the primitive type of stele, at least in these four phyla, was an exarch protostele. Further, though pitted tracheides do not occur in existing Lycopods, they were recorded from *Sigillariopsis Decaisnei* by Renault (38). Thus both anatomically and histologically the Lycopods appear to be constructed on the same ground plan as the Sphenophyllales, Psilotales and Equisetales. In support of the independent origin of the Lycopod, Fern and Horsetail sporophytes, Dr. Campbell relies on the fact that in *Equisetum* the vascular bundles are developed from the "cortical" region of the apical meristem (13). But Dr. Schoute's very thorough researches seem to show that

(except perhaps in certain roots) there is no sharp delimitation of morphologically distinct tissues at the meristem (32). Professor Bower (10) and Dr. Jeffrey (21) also hold the view that apical segmentation affords no proof of the morphological nature of a tissue.

Much discussion has centred round the primitive microphylly or megaphylly of the phyla. In 1903 Dr. Jeffrey suggested a division of the Pteridophyta into Pteropsida (including the Ferns) (20) and Lycopsida (including the Equisetales, Lycopodiales and Psilotales). The Pteropsida, though distinguished also by other characters, were regarded as palingenetically megaphyllous and the Lycopsida as palingenetically microphyllous; it was asserted that in the former the departing leaf-trace left a gap in the stele, while in the latter the gaps in the stele were ramular (20). In 1903 Professor Lignier brought forward good evidence that the numerous simple leaves of *Calamites* and of species of *Sphenophyllum* represent the ultimate lobes of a smaller number of compound leaves found in *Archæocalamites* and other species of *Sphenophyllum*, and that these smaller-leaved forms are descended from species with fewer and compound leaves (28). Dr. Scott, in 1907, accepted this view (34). But Professor Lignier did not extend his explanation of the origin of microphylly in the Sphenophyllales and Equisetales to the Lycopodiales and Psilotales, he asserted that these forms were primitively microphyllous, and that their small leaves, termed by him phylloids, were not homologous with the large leaves of Sphenophyllales, Horsetails and Ferns which alone he regarded as true leaves (28). This view seems utterly untenable for the Psilotales, for Dr. Scott and Professor Thomas have practically established the affinity of these plants with the Sphenophyllales (33), (34), (42), proved by Professor Lignier himself to be primitively megaphyllous. Recent work has shown that the double foliar bundle was no peculiarity of *Sigillariopsis* but probably characteristic of the Sigillariæ generally (1), (24), and if Professor Lignier's contention (in a recent re-statement of his views) that the phylloid as opposed to the true leaf is always unifascicular, and that bifascicular foliaceous emergences are always reduced leaves or lobes of leaves (29) be accepted, then the phylloid theory of Lycopod leaves falls to the ground also. But though this makes it tempting to regard the leaves of Lycopods as reduced, we must remember that the unifascicular leaf of *Lepidodendron* is older than the bifascicular one of *Sigillaria*.

Almost as much importance has been attached to the entry of of a leaf-gap in the Lycopsida as to their microphylly. Dr. Jeffrey has recently asserted that the gap in the wood reported by Miss Sykes (39) at the departure of the sporophyll trace of *Tmesipteris*, and the so-called leaf-gap figured by Professor Bower from the upper part of a stem of this plant (10) have been misinterpreted. Dr. Jeffrey claims that the traces always originate opposite a cauline strand (*i.e.*, leave no gap) but owing to their oblique course they may appear, while in the cortex, to be opposite the gaps; he also urges that these cannot be foliar since they occur mainly on one side of the stele and more than one trace may be related to each gap (21). There is much force in these objections, but as regards *Equisetum* the case is different. Dr. Scott and Dr. Campbell believe that leaf-gaps are present here (34) (13). The latter urges that the gaps between the vascular strands occur alike in branched and unbranched axes and that it is hardly reasonable to suppose that " an ideal branch—so to speak—could cause the development of a ramular gap where no actual branch is present " (13). This refutation of the ramular nature of the gaps in the stele of *Equisetum* seems convincing, and in recently reasserting that these gaps are not foliar, Dr. Jeffrey relies chiefly on the fact that they are not immediately superposed to the departing traces, but are separated from them by the thickness of the " nodal " wood. In the cone he holds that the frequent continuity of the carinal canal through the node proves the absence of a gap (21). The facts are not yet clear—for if the gaps are not foliar it is very remarkable that they should always be equal in number to the leaves; but *if* Dr. Jeffrey's conclusions are correct, the gaps in the stele of *Equisetum* would be neither ramular nor foliar, but more of the nature of the gaps occurring in the rhizomes of many Ferns, to which gaps Mr. Tansley has given the name of perforations. Actually the presence of a leaf-gap is chiefly important, in so far that it supports the primitive megaphylly of the phylum in which it occurs. The absence of a gap in protostelic forms is, as pointed out by Mr. Tansley (41) and Dr. Jeffrey (21), no proof of microphylly, since leaf-gaps cannot occur in a solid stele. The above discussion seems to show that even if they never possessed leaf-gaps, the Sphenophyllales (and therefore probably their allies the Psilotales) and the Equisetales primitively bore large compound leaves; at the same time we have no evidence that the relatively small and simple leaved Lycopods were evolved from forms with large or compound leaves.

The question whether the simple relation of the Lycopodial sporangium to its sporophyll is primitive or due to reduction is a very difficult one. Dr. Scott remarks: "The analogy of the Psilotales rather suggests the latter alternative, and all comparative morphology teaches, how often progress consists in simplification" (34). The same botanist points out, in a foot-note, that the parenchymatous outgrowth bearing the sporangium in *Spencerites* might conceivably be the last relic of the ventral sporangiophore of Sphenophyllales though no trace of vascular tissue has been found in it. Miss Benson has recently reasserted the view that the Lycopod sporangium with its stalk represents a reduced sporangiophore. She gives diagrams of an undescribed Carboniferous *Lepidostrobus*, which she calls *Lepidostrobus Mazocarpon*; the sterile pad of tissue, present in many Lepidostrobi, is here much developed and projects into the sporangium. Miss Benson adds that the divergence of the elongated tapetal cells abutting on the archesporium leads to a split in the median plane of the megasporophyll and that this somewhat suggests a multiple origin of the sporogenous mass. She compares these sporangia to those of the genus *Mazocarpon*; here there is a still larger amount of sterile tissue projecting into the sporangia; according to her figures the upper part of the sporangial wall is also lined by about three to five layers of sterile tissue, between which and the sterile tissue projecting from below, there is, in the median region, only a narrow space. Miss Benson says: "The tetrads are here arranged along the two sides and the space around them was filled with tapetal cells which have perished. One seems to see in this sporange an explanation of the saddle form of many of the 'sporangia' of recent Lycopods, accompanied as such a form is by a well developed 'archesporial pad' .... It would be a very natural sequence that the sporogenous regions of a single sporangiophore should become confluent, and the gradual reduction of the sterile tissue to a mere 'archesporial pad' and pedicel would next follow" (2). On this hypothesis the Psilotaceous synangium would presumably exemplify one of the antecedent stages in the reduction of the sporangiophore with its free sporangia to the Lycopod "sporangium," in which the fusion of sporogenous masses is complete. Professor Bower also regards the Lycopod sporangium as the homologue of the synangium of the Psilotales, but he takes the opposite view to Miss Benson and regards the sporangia constituting the synangium of the latter phylum as the loculi of a septate sporangium (5). Miss Benson's figures of

Lepidostrobus Mazocarpon and *Mazocarpon* might equally well, in accordance with his view, be regarded as stages in a process of the septation of a unilocular sporangium. As evidence in favour of his view Professor Bower claims that in the development of the Psilotaceous synangium, tissue that normally develops as tapetum may become sporogenous and *vice versa*. He also appeals to the incomplete septa found in *Lepidostrobus Brownii* and to the trabeculæ of *Isoëtes* as examples of sterilization leading to partial septation; on Miss Benson's view these structures might be regarded as the reduced remains of former septa. Some support is afforded to the views of both these botanists by the recent description, by Nathorst, of a Rhætic fossil, *Lycostrobus Scotti*, thought to be rather closely related to *Isoëtes*, in which the micro-sporangium was apparently divided by narrow septa (compared by Nathorst to trabeculæ) into roundish loculi (30). The attribution of this fossil, known in a single impression only, to the Isoëtaceous cycle of affinity remains doubtful as no ligule or vegetative organs are known. The weakest part of the theory that the Lycopod sporangium is the result of coalescence and fusion of free sporangia lies in the fact that it is among the heterosporous forms (*Lepido-strobus Mazocarpon, Mazocarpon, Isoëtes*), presumably less primitive than the homosporous types, that what are regarded as the remains of a septum are most strongly developed. On the whole the sterile tissue present in the above mentioned forms is much in excess of that found in *Spencerites* or in most species of *Lycopodium*. Similarly on Professor Bower's hypothesis that the sporangia of the synangium of the homosporous Psilotaceæ represent the loculi of a septate sporangium, it is curious that indications of intermediate stages in the process of septation should be more marked in several hetero-sporous, than in any homosporous members of the Lycopodiales.

The analogy with the Sphenophyllales and Equisetales, in which the ventral lobes of the sporophyll seem (as explained in the first and second articles of this series) to have become free from the dorsal lobes and to have been displaced on to the internode above, makes it possible to regard the sporophylls of Lycopods as lobes of a dorsiventrally lobed sporophyll in which, as in *Spheno-phyllum fertile*, both dorsal and ventral lobes are fertile. But as the oldest known Lycopod fructifications show the same typical simplicity of the sporophyll as the recent cones, and as this Lycopod type is as old as, if not older, than that of any Sphenophyllaceous fructification known to us we should not be justified, in the present

state of our knowledge, in describing the simpler Lycopod cone in the terms of the more complex Sphenophyllaceous ones. Thus. though it seems almost impossible not to regard the Lycopod sporangium as homologous with one or more sporangia of the other Lycopsida the homology of the different parts of the sporophyll of the Sphenophyllales, Equisetales and Psilotales with those of the Lycopodiales remains obscure. Possibly the simple Lycopod sporophyll represents a prior stage of evolution to the apparently primitively lobed sporophyll of the three other phyla, and the subsequent septation of the sporangium into several sporangia and the outgrowth of projections bearing them (sporangiophores) may, as Professor Bower suggests, have given rise to the sporophyll of the Sphenophyllales. The Lycopod sporophyll may, however, have been derived from the dorsiventrally lobed type in either of the ways mentioned above.

To sum up the affinities of the Lycopods: the essential similarity of the sporophyte leaves little room to doubt that this phylum had a common vascular origin with the other Pteridophyta and also that it comes nearer to the other Lycopsida than to the Ferns. But the Lycopodiales differ from the remaining Lycopsida in the structure of their gametophyte, their constant microphylly and the simplicity of their sporophylls. There is some evidence that the peculiarities of the prothallus are an adaptation to a subterranean habit, but little or none as to whether the microphylly and the simplicity of the sporophylls are primitive.

Dr. Scott has said that fossil botany has thrown no clear light on the origin of the Ferns or their relation to other Pteridophyta (33). But as regards their vegetative organs the Ferns show indications of affinity with other phyla. It would seem that, as in the Lycopsida, the primitive type of stele in the Filicales was an exarch protostele, for, for reasons given in the fifth of these articles, the writer cannot agree with Mr. Tansley that the Ferns were primitively endarch. The dichotomous frond seems to be more primitive than the pinnate (31) and the dichotomous leaves of the more primitive Sphenophyllales and Equisetales though smaller and whorled, show a distinct resemblance to Fern-fronds. In this respect the newly discovered *Pseudobornia ursina*, from the Devonian of Bear Island is perhaps intermediate between the Filicales and the other two phyla, for its leaves though relatively large and much divided are whorled (35). Unfortunately its systematic position is uncertain.

Professor Bower has sought to bring the Ferns into relation
with the other Pteridophyta by regarding all the phyla as primitively
microphyllous (9). It has been pointed out above that Professor
Lignier has brought forward good evidence that Sphenophyllales
and Equisetales were primitively megaphyllous (28). In the case
of the Ferns the evidence against primitive microphylly is even
stronger. Nearly all known Palæozoic fern-fronds are relatively
large and compound. Professor Bower claims that the primitive
protostelic ferns show indications of being relatively smaller-leaved
since no gap occurs at the departure of the trace. He also claims
that in its ontogeny the young fern passes through such a stage in
which the trace departing from the protostelic strand leaves no gap
(10). But, as Mr Tansley has pointed out, there can be no leaf-
gaps in a solid stele; thus the absence of gaps in young plants,
still possessing a protostelic cylinder, affords " . . . . no presumption
whatever of derivation from a microphyllous type" (41). In support
of Professor Bower's contention it should, however, be noted that
in the evolution of the Osmundaceæ there seems to have been an
increase in the importance of the leaf compared to the stem, for in
the older Osmundaceæ with tubular steles the departing trace seems
to have left no gap, while in the later forms such gaps occur (25).
This is, however, an isolated instance and there is nothing to prove
that even in the Osmundaceæ the leaves were primitively small or
simple.

But while a comparison of the vegetative organs of the Ferns
with those of the older Sphenophyllales and Equisetales seems
legitimate, it is hard to harmonize their sporangiferous members.
Professor Bower makes of the Ophioglossaceæ an independent
phylum; he holds: (*a*) that their spike arose by the septation of a
sporangium of the Lycopod type; and (*b*) that the sorus of other
Ferns was also derived, though independently of the Ophioglossaceæ,
by septation from a single sporangium; the synangial state, on his
view, represents an intermediate condition, in which the walls
separating the loculi are septa (6), (7).

In seeking to prove the homology of the Ophioglossaceous
spike and the Lycopod sporangium, Professor Bower relies on the
similarity of position, of structure and of development of the spore-
producing parts and on comparisons of gametophyte and gametangia,
embryology and anatomy of the sporophyte in the respective phyla,
and on the intermediate nature of the Psilotaceous synangium (6).
It is surprising that Professor Bower should write that owing to its

constancy he is inclined to attribute considerable weight as a morphological character to the median position of the sporangium on the adaxial surface of the sporophyll in the Lycopods (6), for in discussing the position of the sporangium in *Selaginella* he wrote as follows: "The mere fact that there is variety within the genus in this much discussed and greatly overrated character, should show sufficiently that, however interesting its morphological bearings may be, it is not a point of much systematic importance" (5). Further, in asserting the non-foliar character of the Equisetaceous sporangiophore, Professor Bower has pointed out that similarity of position is no proof of homology, quoting as examples prickles and leaves, both arising from similar tissues of the axis (5). The similarity of form, admitted not to be so obvious, seems very slight; in Professor Bower's figure of the sporangium of *Lycopodium carinatum*, it is enhanced by the shading of the extremities only of the sporogenous mass (6). This shading gives a fallacious appearance of two sporogenous masses, somewhat separated from one another as are the sporangia of *Ophioglossum*. As pointed out in the preceding article the frequent pinnation of the Ophioglossaceous spike and the presence of laminar expansions beyond the sporangia in *Helminthostachys* are evidence of the frond-like nature of the spike. Professor Bower regards the sporangiferous projections of *Helminthostachys* as outgrowths, through which vascular bundles run to the bases of the former loculi of a septate sporangium. No such character as the approach of the vascular bundle to the base of the sporangium is characteristic of the Lycopods and this view seems terribly strained. Again, the similarity of the development of Lycopod sporangium and Ophioglossaceous spike is not very close.

It has already been pointed out, in dealing with the affinities of the Lycopods, that in spite of its radial symmetry, the gameto-phyte of the Ophioglossaceæ is probably not closely related to that of the Club-Mosses. As Dr. Lang notes the antheridia are essentially of the same type in all Pteridophyta (26); but the presence of a basal cell in the archegonium recalls the Marattiaceæ rather than the Lycopods (12). As regards the similarity of embryology of the Ophioglossaceæ the first result of germination, after the division into octants, is a cell mass in which the primordia of stem and cotyledon are not distinct (11), (6). This makes an accurate comparison of their embryology with that of the Lycopods difficult, but the absence of a suspensor and the early development

of the roots in the Adder's Tongues, though not decisive against, cannot be held to favour a Lycopodial affinity.

Endarchy and medullated monostely occur in different members of the Lycopod phylum, but the combination of these two characters, though conceivable also in the Lycopods, is much more filicinean than Lycopodial. The presence of foliar gaps in the Ophioglossaceous stele is also a character of some importance anatomically, for whether or not foliar gaps are confined to the Ferns among Pteridophyta, they appear to be absent from the Lycopodiales (21). The monarch roots of *Ophioglossum* seem to have been reduced from diarch ones (3); this weakens the force of a comparison with those of the Lycopodiales, among whom monarchy, if not primitive, is more widely spread than in the other phyla.

Lastly, the argument resting on the intermediate nature of the Psilotaceous synangium is much weakened if we recognize, as Professor Bower does in his later publications (9), (10), the affinity (to be discussed later) of the Psilotaceæ to the Spenophyllales; for, if the stalked synangium is the homologue of the sporangiophore there is no need to account for the plurality of sporangia by septation, since pluri-sporangiate sporangiophores occur in the Spenophyllales. Of course the conception of the origin of a group of sporangia by septation of a single one might be extended to those Spenophyllales in which the sporangiophore bears more than one sporangium; but as the sporangia of these fossil forms seem to have been normally free from one another, it seems gratuitous to regard the cohesion of the sporangia in their recent allies, the Psilotaceæ, as an intermediate stage between the septation of a single sporangium and the development of its loculi as free sporangia.

We must now briefly consider Professor Bower's view of the derivation of the Ferns (excluding the Ophioglossaceæ) from a primitive type not unlike that characteristic of the Lycopods. His view hypothecates: (*a*), the origin of the synangium by septation of a single sporangium (5), (6); (*b*), the priority of the Fern synangium over the sorus with free sporangia (7) and (*c*), the primitiveness of ferns with small and simple leaves (7), (8), (9). The questions of the origin of the synangium by septation and its priority over the sorus of free sporongia really stand or fall together, for if the latter preceded the former the synangium may presumably be regarded as formed of coalescent sporangia. As already pointed out in discussing

the Marattiaceæ, many Palæozoic synangia probably belonged to Pteridosperms; in this group, apparently so closely related to the ferns that their microsporangia when preserved isolated cannot be distinguished from fern sporangia, the balance of evidence seems to show that the synangium was a derivative condition (23). In recent ferns synangia are normally found only in the Marattiaceæ, and though the cryptogamic nature of the numerous Palæozoic synangia is doubtful, it would seem that if these fructifications belonged to Ferns they are more probably to be assigned to such complex forms as the Psaronieæ, than to the more primitive types such as the Botryopterideæ, though in this respect the synangial *Corynepteris* may prove to be exceptional. Thus the geological evidence is opposed to the primitiveness of the synangium of the Ferns; it is still more strongly opposed to the hypothesis that fern-leaves were primitively small or simple. The evidence on this point has been given in the earlier part of this article and needs no recapitulation. The view that the sorus is the homologue of the sporangiophore is not, however, bound up with the primitive microphylly of the Ferns. Miss Benson, for instance, regards the "sorus" of the ferns as the homologue of the sporangiophore of the Lycopsida, in which category of organ she includes, as explained above, the stalked sporangium of the Lycopods. Yet she assumes the primitiveness of megaphylly, since she states that *Psuedobornia* seems to be a type of probably Calamitean affinity in which the microphylly of the Lycopods had not been evolved (2). As she regards the Lycopod "sporangium" as composed of two completely confluent sporangia she would presumably consider the synangial type of fructification as less primitive than the sorus of free sporangia and leading from the latter to the Lycopod type. If the sorus be regarded as the homologue of the sporangiophore such a view (leaving out the doubtful question of the synangial nature of the Lycopod sporangium already discussed in connection with the affinities of that phylum) would appear preferable to Professor Bower's, since it is in accordance with the primitive megaphylly of the Spenophyllales and Ferns, and with the priority of the sorus of free sporangia, both of which are supported by the geological record. But on either view it is hard to account for the position of the sporangia; in the ferns they are borne on the lower surface or on the margin of the frond or of the branch of the frond, while in all other Pteridophyta they are borne on or near the upper surface of the appendages. In this respect *Cingularia*, probably one of the

Equisetales, may prove to be interesting; for its sporangia appear to have been borne on the lower surface of small sporangiophores. Unfortunately the interpretation of this cone, known only in impressions, is doubtful. If the marginal position of some Fern sori is primitive, the sporangia have in most ferns undergone shifting —such shifting has actually been traced in certain Polypodiaceæ (10). A similar shifting in other directions might have brought about the adaxial position of the Sphenophyllaceous sporangiophore or have produced a marginal and abaxial position of the sorus from an adaxial position. If Mr. Tansley is right in regarding the branching of the frond of many Botryopterideæ in more than one plane as a vestige of a primitively radial construction the branching of the sporophylls of some Sphenopyllales in the dorsi-ventral and lateral planes may be an indication of primitively radial symmetry. Such radially symmetrical sporangiophores occur in the Equisetales, and if primitive, a point in favour of which we have little or no evidence, they might afford an explana-tion of the different position of the sporangia in the Ferns and Lycopsida, since in acquiring dorsiventral symmetry the appendage might well cease to form sporangia on the upper surface in one case and on the lower in the other. All such suggestions are of the most tentative, not to say imaginary nature, and even the homology of the " sporangiophore " and " sorus " which gave rise to them is but a doubtful hypothesis in favour of which we have as yet little evidence.

Professor Lignier regards the matter from a different stand-point. He has drawn attention to the large size and dichotomous venation of the leaves of the more primitive Sphenophyllales and Equisetales, to the fern-like nature of the spermatozoids of the latter phylum and to several less important points indicating, as already noted, a certain affinity between the Equisetales and Spheno-phyllales, constituting Professor Lignier's group of the Articulatæ, and the Ferns. His suggested derivation of the fructifications of the Sphenophyllales and Equisetales from a filicinean type is less convincing. As already explained Professor Lignier has shown that the species of *Sphenophyllum* with small and simple leaves were probably evolved from forms with a smaller number of more highly compound leaves by the precocious division of the leaf-trace within the tissues of the stem, and by the subsequent separation of the lobes of such leaves round the periphery of the stem so as to simulate whole and independent leaves. He has brought forward

evidence to show that the number of these compound leaves in a whorl was primitively three. Professor Lignier takes a similar view of the sporophyll of the Sphenophyllales, and believes that even where most often divided, the sporophylls of this phylum represent lobes of three more highly compound fertile leaves which have become secondarily free from one another in a way analogous to that described above. Thus we gain the conception of a small number of relatively large compound sporophylls not unlike fronds, especially if we bear in mind Professor Lignier's contention that the whorling of the leaves of the Sphenophyllales presumably caused a certain reduction in their size (28). In seeking for ferns from which to derive these Sphenophylls with frond-like sporophylls, Professor Lignier selects the group of fossils known as Archæopterideæ (29), refusing to recognize Mr. Kidston's reasons for regarding these as Pteridosperms rather than as ferns (23). The prevalence of the Pteridosperms, or at least of the Cycadofilices (for the latter may not all have been seed-bearing), in the older deposits in which fern-stems relatively rare, speaks strongly for Mr. Kidston's view; but even if the latter be accepted it is not unlikely that these older Cycadofilices or Pteridosperms may have inherited from the ancestor they presumably share with the older Ferns certain primitive soral characters. Thus it is probable that the sporangia of the ferns were primitively, as Professor Lignier contnds, relatively large and exannulate, and they may have been inserted singly or in small numbers at the ends of the veins (28), (29). To these supposed primitive ferns Professor Lignier applies Mr. Arber's name of Primofilices (as being a wider term than Archæopterideæ); but he uses it, as he points out, in a very different sense, since he regards the Primofilices as the group that gave rise not only to the recent ferns, but to the Pteridosperms and his Articulatæ (Equisetales and Sphenophyllales). The sporophyll of the Sphenophyllales is then regarded by Professor Lignier as the lobe of a frond; its divisions as lobes of the second or higher orders and as pinnules; of these pinnules the median sterile one alone is supposed to remain laminar, while the two lateral sporangiferous ones, reduced to a midrib bearing one or two terminal sporangia, are regarded as displaced on to the adaxial surface where they constitute the sporangiophores. In support of such shifting, which sometimes causes the sporangiophores to assume the appearance of an independent whorl superposed to the sterile one, Professor Lignier claims that the bundles supplying the sporangiophores are inserted laterally on the bundle

of the sterile lobe (28). In the absence of vegetative organs he hesitates to draw any conclusions as to the morphology of the cone of *Cheirostrobus*, but he suggests tentatively that its more bulky sporangiophores may be formed by the coalescence of two lateral lobes comparable to the sporangiferous peduncle of *Sphenophyllum Dawsoni*. These theories of Professor Lignier are ingenious and suggestive, but though the conception of a few highly compound frond-like leaves as the primitive type of sporophyll in the Sphenophyllales seems helpful, there is little in support of the view that the adaxial position of the sporangiophores is due to shifting. A dorsiventral division of the sporophyll is a marked character in such different types as *Palæostachya*, *Calamostachys*, *Cingularia*, *Cheirostrobus*, *Sphenophyllum Dawsoni*, *S. fertile* and *Bowmanites Roemeri*, and it is thus not unlikely that it is a primitive character. But even if we hold to a filicinean affinity for the Sphenophyllales, it is not necessary to regard the adaxial position of the sporangiophores as due to displacement, for in many Botryopterideæ the fronds branched in more than one plane, and it has been suggested that this was a primitive character. But whatever view we take on such points points of detail there remains a wide gulf between a fertile fern-frond and a sporophyll of any known Sphenophyll.

In the same way Professor Lignier seeks to bring the fructifications of the Equisetales into relation with those of the Ferns. The more massive sporangiophores of such a type as *Calamostachys* are regarded as bisporangiate pinnules displaced to an adaxial position and coherent in pairs to form a quadri-sporangiate peltate sporangiophore. These sporangiophores are frequently inserted half-way between two sterile whorls, and such a position is regarded as due to concrescence of the lower part of the sporangiophore with the axis of the spike. Whether or no the adaxial position of the sporangiophores is due, as Professor Lignier claims, to shifting there is some probability, from an analogy with *Cheirostrobus* and *Sphenophyllum fertile*, that the sporangiophores are lobes of the sporophylls, and that their position on the axis is secondary. Mr. Hickling's researches show, however, that *Palæostachya* can no longer be regarded as an intermediate form (18). The view that the peltate sporangiophores of *Calamostachys* or *Calamodendrostachys* represent two coalescent sporangiferous pedicels of *Sphenophyllum Dawsoni*-type is open to grave objections. Not only does the course of the vascular strand of the sporangiophores afford no indication of a double origin, but they are most naturally compared to those of

Equisetum. The radial symmetry of these latter and the fact that not only do they bear more numerous sporangia than most Calamarian sporangiophores, but that in certain Mesozoic *Equisetales*, closely resembling the recent *Equisetum*, there were sometimes over twenty sporangia on a sporangiophore (16), make it difficult to regard the sporangiophores of *Equisetum*, either as composed of two coalescent stalks bearing few sporangia, or as the ultimate sporangiferous pinnules of a fern-frond. Professor Lignier seems to feel this difficulty, for he says that the cones of *Archæocalamites* and *Equisetum* are both of a kind for which it would be rash to give an explanation; he adds that the appendages of the cones do not seem to show a division into fertile and sterile lobes of the second order, but appear to have been transformed as wholes into sporangiophores, or that such a cone as that of *Archæocalamites* may have been derived from a form with alternating fertile and sterile whorls by the abortion of the latter. That this abortion should be so complete as to leave no trace of the sterile whorls, even in so old a type as *Archæocalamites*, seems very unlikely. The hypothesis of the primitiveness of the *Sphenophyllum fertile*-type of cone seems to offer a more natural interpretation; if the dorsal and ventral lobes of the sporophyll of such a type became free from one another and came to be arranged in successive whorls on the axis (as appears to have been the case in *Calamostachys*, where, however, the dorsal lobes had been sterilized), we should get superposed whorls of sporangiophores. Further arguments in favour of such a view have been given in the first and second articles of this series.

The affinity between the Sphenophyllales and Equisetales seems clear. Anatomically the presence of some centripetal xylem in *Protocalamites pettycurensis* is important, for it suggests that the older Equisetales, of whom we have no record, may have possessed an exarch protostele (like that of the Sphenophyllales) in which, in the course of evolution, the centripetal wood was, as it often seems to be, replaced by pith, probably owing to the acquisition of centrifugal wood. In both phyla the leaves seem primitively to have been large, dichotomous and arranged in superposed whorls (34). This superposition, constant so far as we know in the Sphenophyllales, was characteristic also of *Archæocalamites*, of the older *Calamites* (21), and of some Mesozoic genera (36), but has been lost by most species of *Calamites*, by *Equisetites* and *Equisetum*. The strobili consist of whorls of sporophylls and there seems some

probability that in the primitive members of both phyla the sporo-phylls were divided into dorsal and ventral lobes, the lobes being sometimes divided laterally into segments. In both this dorsi-ventral division of the sporophyll seems frequently to have been obscured by the separation of the lobes and by the sterilization of the dorsal ones. It is true that since Mr. Hickling's researches *Palæostachya* can no longer be regarded as a link between the Sphenophyllales and *Calamostachys*, but, as Dr. Scott says, "the evidence of *Calamostachys* itself is sufficient to establish a clear relation between the Calamarian fructifications and those of the Sphenophyllales" (34). The Devonian *Pseudobornia* may probably be another link, for its whorled sporophylls resembling reduced leaves suggest comparison with the Sphenophyllales, its probable heterospory rather recalls the Equisetales, while in the super-position of its large compound leaves it resembles both *Archæo-calamites* and many Sphenophyllales. In their protostely and in the constant superposition of their leaves the latter phylum seems to be the more primitive, while the writer believes that the sporophylls of *Sphenophyllum fertile* are more primitive than those of any Equisetales. Nevertheless, Dr. Campbell, in recognizing the affinity of the two phyla, remarks that according to the geological record " . . . the solid stele of *Sphenophyllum* is a more recent development than the separated vascular strands of the typical Equisetales, as exemplified by *Archæocalamites*" (13). If the hypothesis of the primitiveness of the protostele rested only on its occurrence in the Sphenophyllales it would be weak indeed. Actually, however, this assumption is based on the prevalence of protostely in the simpler members of all the phyla except the Equisetales, on the traces afforded by *Protocalamites pettycurensis* of a derivation of this phylum, also from forms with solid steles, and on the greater proportion of protostelic vascular plants in the Palæozoic rocks than at the present day. It is perhaps strange that Dr. Campbell should attach so much importance to the absence of undoubted species of *Sphenophyllum* from the Devonian and older formations, for he advocates the view that the Ophioglossaceæ are the most primitive Pteridophyta, and however weak the geological record of the Sphenophyllales, it appears to be over-whelmingly strong compared to that of the Ophioglossaceæ.

　　This view of the relative primitiveness of the Sphenophyllales is borne out by the fact that they form a link connecting such different groups as the Equisetales and Psilotales. The affinities of

the latter have been, and still are, the subject of much discussion. Numerous theories as to the structure of these plants and their affinities, varying more or less in detail, have been put forward; these may be divided into three groups: (*a*), Professor Lignier's view that the Psilotaceæ are related to the Lycopods and are quite distinct from the Sphenophyllales; this botanist regards the synangium and its stalk as a cauline structure bearing two phylloids or scales homologous with the leaves of the Lycopods, but not with those of other Pteridophyta; (*b*), that of older botanists, such as Goebel and Strasburger, who regard the synangium as terminal on an axis bearing two fused leaves; this view has been re-stated quite recently in a slightly different form by Miss Sykes (39); (*c*), the synangium is also regarded as a leaf-borne organ, a view held with various modifications by Graf. Solms Laubach (37), Professor Bower (5), Mr. Vaughan-Jennings and Miss Hall (22), M. Dangeard (14), Dr. Scott (34) and Professor Thomas (42).

Anatomically the Psilotaceæ agree fairly well both with the Lycopods and the Sphenophyllales, but as already pointed out Professor Lignier's distinction between the phylloids of Lycopods and Psilotaceæ and true leaves falls to the ground if his own criterion of the constantly unifascicular nature of the phylloid is applied to the Lycopods. Further the Psilotaceæ are, as Dr. Scott points out, too obviously reduced to be regarded as perpetuating the characters of a series forms in which the true leaf, found in the oldest known Ferns and Horsetails had not yet been evolved. This view also neglects the similarity of the Psilotaceæ to the Sphenophyllales made clear by Dr. Scott (34) and Professor Thomas (42). The former has pointed out that the position of the sporangiferous pedicle on the ventral surface of a leaf or sporophyll is closely similar to that of the sporangiophore in the fossil phylum. Further the trace that enters the supposed sporophyll divides into three bundles of which the median one enters the pedicel of the synangium while the two others enter the forks of the sporophyll. Thus the relation of the vascular supply of the pedicel of the synangium to the trace is essentially that of the sporangiophore to the sporophyll in such a form as *Sphenophyllum Dawsoni* or *Cheiro-strobus* though there are necessarily differences in detail owing to the different numerical proportions obtaining between the sporangio-phores and the subtending sterile lobes. This relationship and the compound sporophyll are very different from anything known in the Lycopod fructifications. The abnormalities recorded in considerable

abundance by Professor Thomas (42) in which the sporophylls showed repeated dichotomy, accompanied by the presence of a stalked sporangium at the angle of a dichotomy, also suggest reduction from a more compound sporophyll. Dr. Scott claims that such repeatedly dichotomous sporophylls " are so frequent as clearly to fall under the head of normal variations " (4). He regards them as fatal to a near affinity to the Lycopods and as strong support of a relationship to the Sphenophyllales. Other abnormalities have been reported by Miss Sykes which seem to favour the axial nature of the synangium and its pedicel (39) ; but the importance to be attached to abnormalities depends chiefly on their commonness, unless they are of frequent occurrence they may probably be regarded as malformations rather than as atavistic. There seems no evidence that these abnormalities are by any means as common as those favouring the view that the synangium is leaf-borne. The homospory of the Sphenophyllales favours the view that the Psilotaceæ may have been reduced from them and this view also receives support from the presence of what appears to be the reduced remains of secondary xylem in *Psilotum* (4), (15). But apart from the question of any affinity with the Sphenophyllales and in support of the synangium being leaf-borne Professor Bower has confirmed (5) Graf Solms Laubach's observation that the synangium arises from the upper surface of the "sporophyll" and is not terminal, though as the former points out the lateral or terminal position of the synangium hardly affects the question, since it seems just as probable that a synangium may occupy the apex of a leaf as of an axis. Miss Sykes the latest defender of the view that the synangium is axial admits its probable homology with the Sphenophyllaceous sporangiophore, regarding the latter also as primitively cauline. She suggests that the series of forms, *Sphenophyllum Dawsoni, Palæostachya, Calamostachys*, constructed by M. Lignier to show the shifting of sporangiophore on to the axis, might equally well be read in the inverse order, and would then illustrate the gradual removal of the sporangiophore from the axis to the sporophyll. The fact that *Palæostachya* appears to be derived from the *Calamostachys*-type certainly favours this view. But the origin of the sporangiophore trace of *Calamostachys*, shown in her text-figure 13B (39) from the same point as the bract-trace is somewhat opposed to her view. Further, as pointed out in the first article of the present series, such a theory offers no explanation of the structure of *Sphenophyllum fertile*. If the sporangiophores are

cauline in the Sphenophyllales, the dorsal lobe of the sporophyll of
S. fertile must also be cauline, since the sporangiophores of which it
is composed appear to be identical with the ventral ones; but it is
difficult to doubt the homology of the dorsal segments of the sporo-
phyll of *S. fertile* with the leaf-like dorsal segments of *Cheirostrobus*,
or of such a form as *S. Dawsoni*. These dorsal segments are
termed bracts by Miss Sykes. In the case of *Tmesipteris* Miss
Sykes has shown that the bundle entering the synangium divides
into three, of which the lateral ones run round the periphery of the
septum, while the third terminates in the pedicel. She adds:
" The central trace, described now for the first time, seems an
important piece of evidence in favour of the axial theory of the
sporophyll in the Psilotales, and is here regarded as representing
the vascular supply of the apex of the branch " (39). Such a third
bundle might, however, equally be regarded as evidence of reduction
from the Sphenophyllales, since in *Cheirostrobus* and *Sphenophyllum
fertile* (which on other grounds are probably primitive) the ventral
sporangiophores as well as the dorsal bracts were branched.
Another difference between the sporophyll traces (fertile branch-
traces of Miss Sykes) and leaf traces in *Tmesipteris*, recorded by
Miss Sykes, is the presence at the departure of the former of a gap
in the stele, not occurring at the departure of the latter. Dr.
Jeffrey, after an examination of her slides, asserts that in neither
case is there a gap (21). It is fair to add that Miss Sykes attaches
little or no importance to this difference, regarding it as due to the
earlier preparation for the formation of sporophyll traces (39).

But even if we accept the affinity suggested between the
Sphenophyllales and Psilotales, founded on the homology of the
stalked synangium with the sporangiophore, but supported by other
similarities, we must remember that in the Sphenophyllales the
leaves were whorled, the fructifications, strobili and the stem
branched monopodially, while in the Psilotaceæ the leaves are
alternate, the fructifications non-strobiloid, and the stem branches
dichotomously. It is curious that this last character, often regarded
as primitive, should not be found in the fossil phylum (31). These
differences indicate that the common stock of the two phyla lies
very far back.

Dr. Hallier's views of the affinities of the phyla are in such
marked contrast to those of other botanists that it appears
preferable to notice them briefly and separately. He would derive
all the non-filicinean phyla from the Marattiaceæ (17). His choice

of the Marattiaceæ seems to be largely governed by the fact that their leaves are usually not so highly compound, and their sporangia are exannulate and eusporangiate. The exannulate eusporangiate condition is probably primitive; nevertheless the existence of Palæozoic Marattiaceæ can no longer be regarded as established. The Psaronieæ, the forms most probably related to the Marattiaceæ, seem to have been too complex anatomically to have given rise to the simplest forms of each phylum. For instance, Dr. Hallier derives the Psilotaceæ directly from the Marattiaceæ, regarding their synangia as strictly homologous. Even if, as seems not unlikely, the Psilotaceæ are somewhat reduced, the origin of the protostele locally present in them from a Marattiaceous vascular system seems quite untenable. The Lycopodiaceæ are regarded by Dr. Hallier as derived from Marattiaceous forms allied to the Psilotaceæ (17). Anatomically it is most unlikely that the Lycopodiaceæ should be derived from the Marattiaceæ; from this point of view an affinity between the Lycopodiaceæ and Psilotaceæ has much to recommend it, but as pointed out above, the absence of a sporangiophore in the former makes it doubtful whether the affinity is close. Dr. Hallier holds that the numerous sporangia of a fern-frond have been, in the Lycopodiaceæ, reduced to one; *Pleuromeia* is regarded by him as a primitive Lycopod retaining the numerous sporangia of its fern-like ancestor. But not only is this genus merely of Mesozoic age, but this or any other interpretation of its fructification is very doubtful. The incompletely septate sporangium of *Isoëtes* is regarded as a synangium homologous with the synangium of the Marattiaceæ. The discovery of a form probably allied to *Isoëtes* (i.e., the Rhætic *Lycostrobus Scotti*) with an apparently septate microsporangium favours this suggestion, but even so the single non-septate sporangium appears to be the oldest type among the Lycopodiales. Dr. Hallier recognizes the affinity between the older Equisetales and the Sphenophyllales; he derives them both from the Marattiaceæ. Here again the anatomy of *Equisetum* and still more that of *Sphenophyllum* absolutely forbids such an origin. This scheme of classification seems very unnatural; one of its defects is that Dr. Hallier assumes, to judge from his diagram, that the strobilus originated but once in the vegetable kingdom. But among the Strobiliferæ he includes the Cycado-filices, which we now know not to have been strobiloid; the cones of their descendants, the Cycads, therefore presumably originated separately from, and more recently than those of, the

Horsetails, Sphenophylls or Lycopods, a view supported by the absence of a megasporangiate strobilus in *Cycas*.

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BEANS GROWING "ON THE WRONG SIDE."

IN the autobiographical chapter of the "Life and Letters of Charles Darwin" (Vol. I., p. 104) reference is made to the widespread belief among farmers that in certain years the common field-beans grow "on the wrong side of the pod," or, as it is sometimes more vaguely put, "on the wrong side." Darwin tried to find out what such expressions could mean, but his informants were quite unable to give any explanation. After fruitless enquiries he concluded that it was a case in which "a belief—if indeed a statement with no definite idea attached to it can be called a belief—had spread over almost the whole of England without any vestige of evidence."

It seemed to me hardly likely that an idea of such wide currency should be merely a baseless superstition, and I determined to try and investigate it a little further. Many years ago I asked the question, "Do beans grow on the wrong side in certain years?" of some of our farmers and farm labourers in Bedfordshire. I found that the *younger* men knew nothing of it, but the *older* men all knew of it and "were quite sure it was true because they had known it ever since they were boys," but not one could give me any explanation! I have been unable to get any light on what is exactly meant by the beans, or seeds, growing on the wrong side *of the pod*. One can imagine no meaning for it except that they grow on the dorsal suture, which I believe is an unheard of thing. But on thinking over the life-history of the bean, and my recollections of threshing with the flail before the use of machinery, a suggestion has occurred to me in reference to the beans growing "on the wrong side" *of the stem*, which I put forward for what it is worth. Possibly some of the readers of the NEW PHYTOLOGIST may be able to throw more light on the subject.

In ordinary years it is very noticeable in passing a ripe bean-field that the bean-pods are all on the *south* side of the stems, because when the flowers were out they turned to the sun. This made it very convenient for striking with the flail, since the pods were all on one side standing clear of the stem, and hence lay flat on the floor. But in very wet seasons, if there is no sunshine when the flowers are coming out, they miss the directive influence of the sunlight, and they, and the pods which succeed them, point in all directions, making it very inconvenient for striking with the flail. This might well, in the uncritical language of the farmer, be described as "the beans growing on the wrong side." Now that the threshing is done by machinery, the direction of the pods is a matter of indifference, and hence passes unnoticed, and the tradition which Darwin described as "the oddest case" which he had known, seems in a fair way to die out altogether.

Berrystead,
    Woburn,
       Beds.

E. AVELING GREEN.

NOTES ON RECENT LITERATURE.

FUNGI.

The Cytology of the Uredineæ.

THE Rust Fungi have been a favourite group for cytological investigation in recent years. V. H. Blackman[1] was the first to show that the binucleate condition of forms possessing the Cæoma-type of æcidium arises first in the "basal cells" which later give rise to chains of æcidiospores. He found that a nucleus from the cell below the basal cell migrated into the latter through a pore in the wall separating the two cells. He interpreted this phenomenon as the fertilisation of a female cell by the migration into it of the nucleus of an undifferentiated mycelial cell in default of fertilisation by a spermatium, considered by him a functionless male cell. Christman[2] later described the binucleate condition of other Cæoma-forms as arising by the fusion of two cells undifferentiated morphologically one from the other. These fusing cells he considered to be undifferentiated gametes, the spermatia being interpreted as conidial structures. Blackman however would interpret this occurrence as the fusion of female gametes in pairs somewhat comparable to the fusion which takes place between the female nuclei of the ascogonium of *Humaria granulata.*

In spite of the divergence in the interpretation of these phenomena and the different views held as to the phylogeny of the Uredineæ by the two authors mentioned, there can be no question of the importance of the work done, as they have established quite firmly the existence of an alternation of generations in the Rust Fungi.

Christman's more recent work[3] throws some light on the question of the morphology of the different spore forms of the Rusts. In seeking the origin of the binucleate phase in species which have been described as not possessing an æcidial stage, he has obtained evidence that the primary uredospores of the Brachy-types are to be identified with æcidiospores. The Brachy-types of Schroeter's classification are those which possess all spore forms except the æcidia. It has long been recognised that the uredo pustules of the Brachy-types are of two kinds, *viz.*, those which arise first and are confluent and those which arise secondarily and are scattered. The mycelium of the former which are called the primary uredo pusteles, produces great hypestrophy of the host comparable to the distortion caused in other hosts by the presence of the æcidial mycelium of other Uredines. It has been noted too

[1] Blackman, V. H. On the fertilisation, alternation of generations and general cytology of the Uredineæ. Annals of Botany, 1904.

[2] Christman, A. H. Sexual reproduction in the rusts. Botanical Gazette, 1905.

[3] Christman, A. H. The alternation of generations and morphology of the spore forms in the rusts. Bot. Gaz., 1907.

that the primary uredo pustules are accompanied by spermogonia. On the other hand the secondary uredo pustules are not accompanied by spermogonia. Winter in fact surmised in 1884 that the primary uredo pustules of Brachy-puccinia represented the æcidia of other forms. Christman now finds that the primary uredospores of *Phragmidium potentillæ canadensis* arise from basal cells which become binucleate in the same manner as that described for the basal cells which give rise to the chains of æcidiospores in *Phragmidium speciosum*. These basal cells in the primary uredo pustule of the above species of *Phragmidium* form spore mother cells, each of which by division produces a spore and a small sterile cell which elongates to form the stalk of the primary uredospore. A second spore and stalk are produced by the putting out of a bud from the basal cell and subsequent division. Christman identifies the stalk of the primary uredospore with the intercalury cell of the æcidiospore.

More recently Olive[1] has confirmed for *Triphragmium ulmariæ* the view that the primary uredospores of Brachy-forms correspond to æcidial stages of other types. In the Micro-forms, *Puccinia transformans*, i.e. a species possessing only teleutospores, he finds that the basal cells which produce the teleutospores, arise by the fusion of two uninucleate cells, so that the origin of the teleutospores of this species may be said to be similar to that of the æcidiospores of other forms.

Christman finds also that the secondary uredospores, also of *Phragmidium potentillæ-canadensis* also arise from large basal cells though of course in this case the latter are borne on a mycelium of binucleate cells. The teleutospores of *Puccinia podophylli* arise also from large basal cells. These large basal cells in the developing uredo- and teleutospore pustules have also been described by Blackman in his work on *Phragmidium violaceum.*

Christman is impressed with the similarity between the basal cells from which the uredo- and teleutospores originate and those which give rise to the æcidiospores. He considers therefore that the basal cell is the morphological unit to which may be referred all the other spore forms of the sporophyte generation. According to this point of view teleutospores, æcidiospores, and uredospores would all be considered secondary structures. That there is some essential connection between these spore forms would appear to follow from a consideration of such a genus as *Endophyllum* in which the teleutospores are abstricted in the same manner as the æcidiospores of other genera.

In the paper by Olive cited above, an account of the cytological investigation of the origin of the chains of æcidiospores of other forms is given. Most of this work concerns the Cæoma-type of æcidium with which Olive includes the primary uredo spore generation of the Brachy-forms alluded to already. Olive finds that the binucleate condition arises by the conjugation of two uninucleate cells. In the process of fusion the nucleus and cyto-plasm of the one cell pass into the other cell by means of a pore of greater or less width. Olive mentions the difficulty experienced in

[1] Olive, E. W. Sexual Cell Fusions and Vegetative Nuclear Divisions in the Rusts. Annals of Botany, 1908.

determining the orientation of the fusing cells. He considers that this difficulty, coupled with variability in size of the conjugating pore is sufficient to account for the divergence of what may be called respectively the Blackman and Christman method of binucleate origin. Olive makes mention of a case in which a Blackman "nuclear migration" is found adjacent to a "cell fusion" of Christman's method. Blackman, however, in his paper of 1904 speaks of a distinct difference in size between the migrating nuclei and the nuclei of the cells he considers female cells; nor does the determination of the orientation of the cells seem to be in doubt.

It is of considerable interest that Olive has determined the exact place of origin of the binucleate condition in the Micro-form, *Pucinnia transformans*, to be in the basal cells, which gives rise, almost immediately, to teleutospores. Nevertheless, it is known that in certain Micro-forms the binucleate condition arises much earlier, for Blackman[1] found that the general vegetative mycelium of *Pucinnia Adoxæ* and *Uromyces Scillarium* shewed conjugate nuclei.

In the same paper Olive makes mention of the occurrence of multinucleate cells at the base of certain young æcidia of the type possessing a pseudoperidium. Cells containing more than two nuclei have been described by Blackman as occurring in the young æcidia of *Puccinia poarum*. Æcidiospores of other species pos-sessing several nuclei are of fairly common occurrence. In the young æcidium of *Puccinia Cirsii-lanceolati*, Olive describes cells containing as many as twelve to fifteen nuclei, and in one case he describes twelve nuclei of one cell as undergoing division simul-taneously. He is inclined to think these cells are sporophytic structures and considers that they have an important bearing upon the mode of development of the æcidium cup. Further details of the origin and subsequent history of these multinucleate cells will be looked forward to with interest.

Olive's interpretation of the sexual phenomena at the base of the Caeoma-type of æcidium is the same as that of Christman. Thus he considers the cells which fuse to be undifferentiated gametes. Christman considers the spermatia to be asexual gameto-phytic spores, while Olive practically leaves them out of considera-tion altogether. It seems somewhat extraordinary that cells, which, as Blackman has pointed out, have the cytological characteristics of male gametes, should be dismissed in this way. The similarity between the spermogonia and certain Ascomycetes and those of the Uredineæ merits further consideration than it has yet received. If the spermatia are really functionless male-cells, one can under-stand the frequent occurrence of spermogonia immediately prior to the formation of the primary uredo pustules of Brachy-forms which as we have seen are to be brought into line with the æcidia of other species. F.T.B.

[1] Blackman, V. H. and Fraser, Miss H. C. I., Further studies in the sexuality of the Uredineæ. Annals of Botany, 1906.

THE TEMPERATURE RELATIONS OF FOLIAGE LEAVES

IN a comprehensive paper on the Physical Properties of Foliage Leaves, Ursprung has included, besides a large number of experiments on the mechanical properties of petiole and lamina, some experiments on the thermal properties of leaves, chiefly on the temperatures attained by foliage leaves in the sunlight. The paper contains a valuable survey of previous work, a clear analysis of the factors upon which leaf-temperature depends, and a number of original observations of leaf-temperature. For these experiments he rejects the thermo-electric method instituted by Stahl and uses a mercury thermometer. In the case of fleshy leaves, the bulb was stuck into the substance of the leaf. In the case of thin leaves, it was laid on the leaf surface and the leaf was folded up around it. He obtains very high temperatures for thick succulent leaves such as those of different species of *Sempervivum*. These attained internal temperatures of from 48-52° C when the shade temperature of the surrounding air was 12-16° C. In other succulents, e.g., *Opuntia Rafinesquii, Saxifraga crassifolia* he obtains the high temperatures of 43° and 36° C respectively. For thin leaves *Betula alba* and *Ulmus montana* he obtains temperatures of only 28° and 29° respectively. From Angot's figures of radiation at the equator he concludes that high internal temperatures in succulent leaves in the tropics must often occur, and therefore these temperatures cannot be so injurious as earlier observers, *e.g.*, De Vries and Sachs, supposed.

With regard to the effect of colour on leaf-temperature he makes the general statement that the decrease of diathermancy, due to the presence of anthocyan masking the green colour of a leaf, must tend to raise its internal temperature.

The chief defect of his method is the use of a mercury thermometer by which the internal temperature of a thin leaf cannot be obtained. What is obtained is the surface temperature, in determining which, other factors, chiefly those causing heat loss by convection and radiation, play a greater part than in the case of true internal temperatures.

Blackman and Matthaei, 1905, introduced an improved form of thermo-electric junction which was small enough to be inserted in a thin leaf and brought out the unexpected fact that even thin leaves attained very high internal temperatures, 45° C being reached by a cherry-laurel leaf exposed to direct radiation from the sun at noon in July.

This thermo-electric method has been used more recently by Baumert in investigations as to the various methods by which leaves protect themselves from too intense light. As source of light he used a constant petroleum lamp, the light from which fell on the leaf in a moist chamber at an angle of 45°. The temperature was measured by a small thermo-junction of needle form to which was attached a D'Arsonval galvanometer. In this way he compared the temperature attained by leaves with, and leaves without, a protective covering of different kinds, *e.g.*, a covering of hairs, a covering of wax, a glossy upper surface, a wet upper surface, stratification of outer epidermis wall as in species of Ferns, &c. In the

case of leaves with a waxy covering he compared the normal leaf with one stripped of its waxy covering, but in the case of a glossy leaf he could not compare with one stripped of its upper epidermis and therefore used as control the dull under surface of a leaf of the same species. This introduced an error which somewhat vitiated his work, in that he did not seem to realise that the under surface was usually stomatal, the upper non-stomatal, and thus the difference obtained was probably not solely to be traced to the different power of reflection of the two surfaces, but partly to the greater transpiration from the under surface having a cooling effect. Since, however, the temperature was higher when the under surface was exposed, the result obtained is probably genuine. He made attempts to avoid the error due to difference of evaporation by shortening the time of exposure, so that the temperature of the leaf should not much exceed that of the air around, but the error still probably remained considerable.

The comparison given by him of wetted and dry leaves is almost valueless, if the difference is attributed to the different reflecting powers of the two surfaces, since it is probably almost all due to the cooling of the wet leaf by evaporation of the water.

The results show that in each case the covering investigated, hairs, wax, &c., &c., acts as a protection from too great heating by the radiation received. The temperature was always lower when such a covering was present, the difference produced by a thick covering of hairs amounting to as much as $37.5°$ C.

He made no experiments on the effect of different colouration of leaves, *e.g.*, leaves containing anthocyan.

A contribution from a different point of view was recently made by Molér, who quoted Tischler's view that red colour was an adaptation for a severer climate in that leaves better provided with reserve material were able to withstand frost better. He thought that the red forms were better adapted for assimilation and stored up more reserve. Molér found in opposition to this that the red forms are more sparsely provided with chlorophyll. By means of a special spectroscope he could obtain side by side the spectra of two solutions lighted by two equal lamps. On thus comparing the chlorophyll solution from a normal green leaf and from a leaf of the same species containing anthocyan under equal conditions, he invariably found the chlorophyll weaker in the red leaf. The apparatus is not fully described in this preliminary note, but he does not state whether he first of all got rid of the anthocyan or whether it remained to disturb the effect of the chlorophyll solution obtained from the red leaf.

The results when fully obtained will be valuable not for the light they throw on Tischler's unimportant theory, but because we shall have some quantitative idea of the total amount of absorbing pigment, whether red or green, in a leaf containing anthocyan, compared with that in a green leaf of the same species.

Wiesner has described experiments carried out to establish the protective effect of division into small parts, or of a form, such as that of a linear leaf, where the surface is very great relative to the volume, upon the internal temperature of such finely divided or linear leaves or plant parts. He placed at the focus of a powerful convex lens exposed to clear sunlight a number of experimental

objects.   Twenty-five awns of barley were first taken and bound in a bundle.   These ignited in three to four seconds.   A single awn remained unburnt for over four minutes.   Similar results were obtained with fresh shoots of *Asparagus plumosus.*   A single phylloclade remained unburnt for five minutes, while a shoot with several phylloclades together ignited immediately.   Like results followed from comparison under similar conditions of a large phyllode of Acacia and a small leaf of Erica, the phyllode burning in nine seconds, the leaf taking forty to fifty seconds.

Wiesner ascribes this difference by which small parts remain lower in temperature, not to a difference in the excess of absorptive power for heat over loss of heat by radiation, but to the much greater conduction of heat from the relatively large surface of the small parts, combined with the greater diathermancy caused by their thin texture.

As supporting this opinion he describes parallel experiments carried out both with Acacia phyllodes and with Erica leaves, in which in each case the height of the sun was the same, the temperatures as registered by a black bulb thermometer were equal, but the air-temperature was considerably lower in one case than the other.   This caused a very much longer time to elapse before ignition, since now the loss of heat from the surface to the surrounding air at a low temperature was much greater.   Thus small dimensions or fine division of plant-parts prevent a high internal temperature from being attained.

Passing from the environment as conditioning temperature in leaves to the subject of the effect of the activity of the leaf itself on its temperature we note that Molisch has been able to show that a rise of temperature due to respiration can be clearly shown in the case of the leaves of many species.   He gathered large quantities of leaves, taking care that they should be dry, and placed them in a wicker basket.   This was put inside a wooden box, the intervening space being packed with shavings.   The whole was surrounded by several layers of cloth and the top covered by pasteboard through which a thermometer was passed into the leaves.   Quantities of from three to five kilogrammes of leaves were used in each experiment.   The cover was taken off from time to time to examine for the presence of bacteria or fungi and to see if the leaves were still turgid or whether they were discoloured and dead.   The experiments were carried on for several days, in one case for sixteen days, the temperature being read at first hourly, later three or four times a day.

The curve of temperature readings thus obtained had two maxima with lower readings between, e.g., in *Carpinus Betulus* the temperature reached $51 \cdot 5^{\circ}$C after fifteen hours.   It then sank to 34° after forty-eight hours. It attained its second maximum of 47° after 104 hours and then gradually sank to 31° after 180 hours. This was a typical curve.   By examination it was ascertained that at the first maximum the leaves were living and almost free from bacteria or fungi.   The high temperature therefore was due to respiration.   It killed the leaf and then the temperature began to fall.   The second rise could clearly be attributed to the action of bacteria and fungi, as at its height the leaves were covered with these organisms. Leaves vary very much in the temperature they attain under these

conditions, *Pirus communis*, for example, reaching 44°C above the surrounding air, while *Hedera helix* only reached 6·6°C and succulent leaves of *Bergeria* only 3·5° above the surrounding air of the room.

Molisch attributes this to the sluggish respiration occurring in succulent and stiff leaves. He does not, however, make any confirmatory measurements of the rate of respiration in his leaves. He carried out experiments proving that the rise of temperature was not due to increase of respiration caused by the wounding of the petiole in cutting off the leaf. He also used wet leaves and found them to rise in temperature much more slowly than dry leaves. This had the effect of bringing the two maxima of the usual curve together to form one. He attributes this slower rise of temperature partly to the effect of water in stopping up the stomata and thus hindering respiration, and partly to the better conduction of heat from the mass when the spaces between the leaves are filled by water and not air. It is more likely that it is principally due to the amount of heat required to slowly vaporise the water at these temperatures.

Though at first sight it is surprising that such high temperatures should be attained due to respiration alone, yet when arrangements are made for preventing loss of heat by radiation, conduction, &c., the slight rise of temperature due to respiration in each leaf must have a cumulative effect, and the temperature will rise until heat gained and heat lost are equal.

When such an equilibrium is attained the temperature will probably be a fairly exact measure of the intensity of respiration. It is interesting thus to find in some cases that the slackening of respiration still occurs, although the first maximal point was below death-point for the leaves. This falling off is attributed by Molisch, with a great degree of probability, to the exhaustion of the carbohydrate reserve at first present in the leaf. An instance of continuous rise in temperature in pear leaves after death-point had been reached, and before the activity of bacteria had set in, is attributed to postmortem breaking-down changes due to the activity of oxidases.

<div align="right">A.M.S.</div>

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THE DISPERSAL OF THE SEEDS OF THE GORSE

AND THE BROOM BY ANTS,

BY F. E. WEISS, D.SC.,

Professor of Botany in the University of Manchester.

[TEXT-FIGS. 1 AND 2.]

I N reviewing Sernander's Monograph of European myrmeco-
chorous Plants,[1] I alluded to the curious distribution of the
gorse (*Ulex europæus*) along roadsides and over disused cart-
tracks on moorlands, and suggested the probability of ants acting
as agents in the dispersal of the seeds of this plant. The fact that
the seeds of the gorse are provided with a brightly coloured
caruncle filled with oily food material and resembling very closely
the elaiosomes described by Sernander[2] for *Chelidonium*, *Viola* and
other plants, the seeds of which are carried away by ants, seemed
to me a strong argument in favour of including Ulex among the so-
called myrmecochorous plants, and as ants are known to make use
of paths and roadways for facilitating the transport of their
building-material and food to their nests, we should obtain an
explanation of the spreading of gorse-bushes along existing and
disused roads.

I mentioned a striking instance of such rectilinear distribution
of gorse-bushes on the high moorland above Wass Bank in York-
shire, where the Ulex extends in a straight line from the main-road,
along which it is well distributed, across a pure Calluna moor, and on
closer inspection is found to mark out the course of an over-grown

[1] Weiss, F. E. The Dispersal of Fruits and Seeds by Ants.
    NEW PHYTOLOGIST, Vol. VII., No. 1, 1908.

[2] Sernander, R. "Entwurf einer Monographie der Europäischen
    Myrmecochoren." Kungl. Svenska Vetenskapsakademiens
    Handlingar, 1906.

moorland cart-track. This instance of singular distribution of Ulex was pointed out to me by Mr. Hugh Richardson, of York. A similar and no less striking case has come to my notice this summer in Derbyshire. Close to Hurdlow Station, which lies about six miles south-east of Buxton on the Buxton-Ashbourne Line, are a number of fields covered with heather (Calluna), such as one meets with here and there on this high Limestone plateau. In this particular case the heather is found to be growing on the chert, which as Sibley has shown is extensively developed in Derbyshire, and often persists to the top of the Carboniferous Limestone.[1]

Dr. C. E. Moss, who has made a careful survey of the vegetation of the Pennine Range in Derbyshire, tells me however that Calluna is by no means confined to the areas in which the limestone has been transformed into chert, but occurs sometimes on the limestone itself. On the " six-inch " survey (1:10560) from which the accompanying map (Fig. 1) has been traced, the presence of Calluna is indicated by the conventional symbol over three large meadows close to the railway-line. In two of these meadows, through which the railway line actually passes, the heather is only found to the west of the line, which follows approximately the lowest level of the undulating land, so that the exposure, and possibly the sub-soil, may be different on opposite sides of the line. On the survey map the presence of gorse (Ulex) is also indicated among the heather, but its distribution is not accurately mapped. Instead of being irregularly scattered as would seem indicated on the survey map, it forms in the field ABDC a very distinct line, AD, running more or less diagonally across the field and in striking contrast to the short heather among which it grows. Seen from the slopes around, it is one of the most conspicuous features of the vegetation, and from a distance the line is so straight that it gives one the impression of a wall or earthwork thrown up in the field. A closer examination of the ground discloses the presence of cart ruts overgrown with heather and gorse, and even now a public footpath exists from the point D across the field to A and thence to the Hartington road, so that the gorse bushes undoubtedly mark out the course of an old roadway across the field ABDC. The gorse seeds have been distributed along this line from the lower meadow ACFE, in which there is a large and irregular patch of Ulex close to the

[1] Sibley, T. F. On the Faunal Succession in the Carboniferous Limestone of the Midland Area. Quarterly Journal of the Geol. Soc., LXIV., No. 253, 1908.

corner A. There are, besides, a few isolated bushes of gorse in the upper field ABDC, but so few that they in no way lessen the
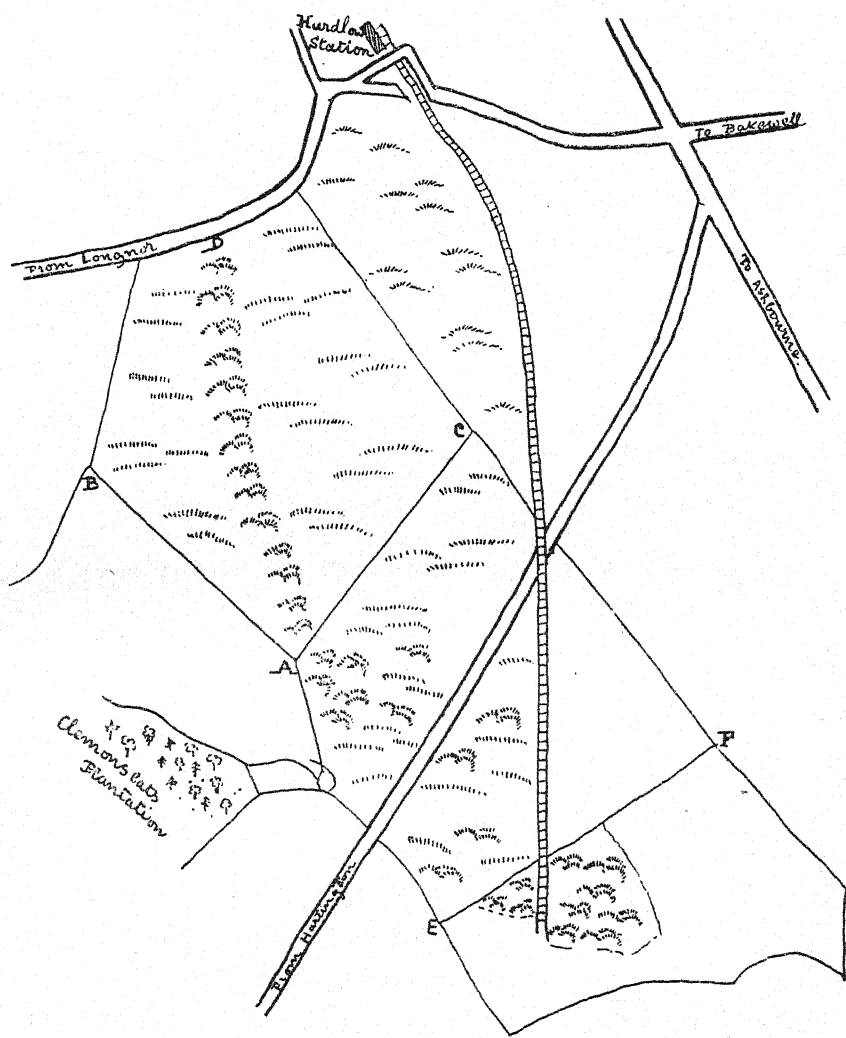
- Ulex

= Calluna.

Fig. 1. Plan of some fields near Hurdlow Station in Derbyshire. Showing rectilinear distribution of the gorse (*Ulex europœus*) across a heather covered field ABDC. (From the six-inch to a mile Ordnance Survey Map. Scale 1 : 10560).

effect produced by the very distinct line along the footpath. I have not been able to discover any existing ants' nest along this line of furze bushes, but as they are all of considerable size and age, the absence of ants now does not preclude the possibility of ants having acted as agents of dispersal in former days.

Another, though a less striking case of the dispersal of gorse along a roadway was noticed in Wales (see Fig. 2), and is mentioned
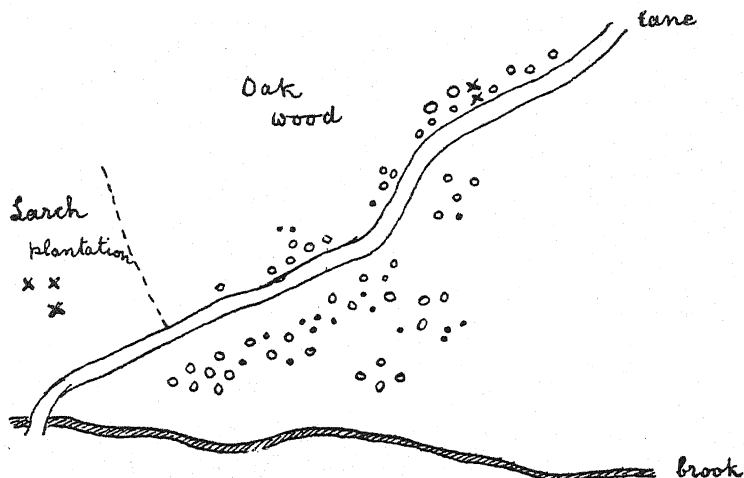
o = gorse (*Ulex*)   • = broom (*Sarothamnus*)   × = ants' nest.

Fig. 2. Sketch plan showing bushes of gorse and broom along a lane near Fairbourne. The distribution has proceeded from the gorse and broom bushes in the triangular meadow, sloping down from the lane to the brook.

here because in this case the distribution of the gorse seemed to be still in progress, many of the bushes being small and the ants being still at work carrying building material and food to their nests, which were close to the roadway, in fact on the bank of the lane. This lane ran up from the main road at Fairbourne, near Barmouth, to a hillside farm. On one side it was bounded by an oak wood with a steep bank, along which in a distance of about fifty yards were two comparatively large and sixteen smaller gorse-bushes. There was also a small plant of broom (*Sarothamnus scoparius*). There was neither gorse nor broom in the oak wood, but on the other side of the lane which was bounded by a loose stone wall, was a steep grassy slope on which were numerous gorse-bushes massed together and interspersed with some broom. Both of these are indicated on

the sketch plan by different symbols. Close to the two larger gorse-bushes at the edge of the wood were two nests of the large Wood Ant, one on the top and one on the slope of the steep bank. The proximity of the line of young gorse-bushes to the roadway and to the ants' nests was suggestive of the seeds having been carried along the lane at the edge of the wood by ants, while the stone wall separating the gorse at the edge of the wood from the main patch on the grass-slope below seemed to preclude the possibility of the seeds having been distributed from the main patch by the explosive contraction of the dry pods. It is of course possible that the older plants at the edge of the wood might have been established before the wall was built, but the appearances were somewhat against this, while on the other hand, the wall was sufficiently loosely built to enable ants to make their way quite easily from the meadow to the lane.

The proof of the part played by the ants in the dispersal of the gorse, must, however, depend on the readiness and ability of the ants to carry the seeds of this plant, and not merely upon such striking examples of rectilinear dispersal as I cited in my previous paper and as the one described above (p. 82). I accordingly made some experiments on the lines indicated by Sernander on one of the tracks along which the ants were passing to and from their nest. On the evening of September 18th, I placed ten seeds of Ulex on one of these tracks and in half-an-hour eight of the seeds had been carried away by the ants. Owing to darkness the experiment had then to be interrupted. On September 19th, I continued the observations close to one of the ants' nests in a small larch plantation shown on the sketch plan.

At 3·15 five seeds of Ulex were placed on one of the ants' pathways.
at 3·20 only three seeds were left;
at 3·25 none were left;
Another experiment with nine seeds had the following result:—

3·30	...	...	...	9 seeds
3·35	...	...	...	8 seeds remained
3·40	...	...	...	5 „ „
3·45	...	...	...	1 „ „

The seed that remained had a shrunk and discoloured caruncle and was left untouched by the ants while the observations were continued. It was unfortunately rather late in the season to obtain undamaged seeds of the gorse, as most of the pods had dehisced and most of the remaining ones were attacked by the maggot of the little weevil, *Apion ulicis*. As it might be thought that the ants would be likely

to remove indiscriminately any seeds placed in their pathway, a control experiment, such as were made by Sernander, was undertaken. The hard brown fruits of the burdock (*Arctium Lappa*) and fruitlets of the Wood Sage (*Teucrium Scorodonia*), both growing in the vicinity, were chosen. The former were larger and the latter smaller than the gorse seeds, but both have a rough surface and would be easier to carry than the smooth and slippery seeds of the gorse. The ants, however, did not touch the fruits of the sage and removed only one of the burdock fruits. This showed that they were capable of removing them, though they seemed to take very little notice of them. Their shape and size would, however, make them quite as convenient for the building of the nest as the other particles of wood and dead winter buds of the oak, which figured so largely as building material.

A table showing the relative activity of the ants may be made as follows :—

	Number of seeds of		
Time	Ulex	Arctium	Teucrium
3·15	5	5	5
3·20	2	4	5
3·25	0	4	5
3·30	0	4	5

The table alone, however, does not represent the whole difference in the behaviour of the ants towards these three units of dispersal, "Verbreitungseinheiten," as Sernander calls them. The majority of the ants, intent possibly upon some definite purpose, passed by or even over the seeds of all three plants, apparently without taking note of them. Those which noticed the fruits of the burdock, made a hasty examination of them and then passed on. But when an ant stopped to examine the gorse seeds, it quickly found the bright orange caruncle and immediately began to bite and gnaw it. After that, it would rarely let the seed go, unless forced to do so by another ant and often two or three would struggle at it together. They generally set the smooth seed up on edge, holding it with their hind legs, and, bending right over it, would apparently endeavour to remove the food-body or elaiosome. Unable to accomplish this, they would after a more or less lengthy struggle carry away the seed, not without some difficulty in getting a proper hold of it, eventually in all cases holding it by the soft and fleshy caruncle.

Even when the caruncle was removed, the seeds were rapidly taken up by the ants, but I think, as Sernander found in the case of some of his experiments, that enough of the oily food-matter

adhered to the seed to render them attractive. That the elaiosome itself is a desirable object to the ants, was easily proved by placing some of the detached caruncles in the pathway and these were readily carried away, when once they were observed. But being very small they were more often overlooked, and this fact would indicate, as indeed the previous experiments had done, that the elaiosome does not attract the ants by any special odour or scent.

When I first made the suggestion that the orange-coloured caruncle of Ulex acted as a food-body or elaiosome for ants, it was pointed out to me that the broom (Sarothamnus) possessed a very similar caruncle which must probably serve the same purpose. Though I know of no striking cases illustrating the dispersal of the broom along disused roadways such as I have instanced in the case of the gorse, yet I noticed, as mentioned above, a young plant of Sarothamnus at Fairbourne which could not have owed its position to the mere dehiscence of the pod, as the nearest presumptive parent was at least twenty feet away and on the other side of a stone wall. Ants on the other hand could have readily effected the dispersal. I consequently made some experiments with the seeds of the broom, similar to those I had made with the gorse-seeds.

On September 20th, I placed five seeds of the broom on an ant-track leading to one of the nests with the following result :—

6·7	...	...	...	...	5 seeds
6·10	...	...	...	...	4 seeds remained
6·14	..	...	...	...	3 ,, ,,
6·16	...	...	...	...	2 ,, ,,
6·21	...	..	...	...	1 ,, ,,
6·25	...	...	...	...	0 ,, ,,

In other words the five seeds had been carried away in eighteen minutes, and the behaviour of the ants had been identical with that exhibited when they found the seeds of the gorse. They turned the smooth seeds about and when they found the food-body they rarely let go, biting and tearing at the elaiosome and finally carrying the seeds bodily away.[1]

The above experiments leave it uncertain whether the ants actually get any large quantity of the seeds they carry away to their nests or whether they manage to sever the elaiosome from the seed on their way. Judging from Sernander's investigations probably some remain by the roadside while some are actually taken to the nests. On one of the ants' nests examined, there were

[1] Mr. A. G. Tansley tells me that he has observed the distribution of the broom together with the gorse along an old cart-track overgrown with heather on a large heather-moor near Rievaulx Abbey in the North Riding of Yorkshire.

several germinated seeds of Ulex, but these and others in the neighbourhood might have got there by the force of dehiscence of the pod, as they were close to a mature gorse-bush. There were other seeds, particularly of grasses, which had germinated on one of the ant-hills, but these may easily have been blown there. I took away with me, however, about as much of the deeper portion of the ant-hill as would fill a litre measure, with a view of examining its seed-contents. This proved somewhat difficult from the many round seed-like particles of earth and wood and the innumerable small dry winter buds of the oak of which it consisted. I found that the best method of sorting out the seeds was to let them begin to germinate and then to pick out the seedlings with the seeds attached. In this way quite a number were separated out, and I had the kind assistance of Miss E. M. Kershaw and of Mr. Clement Reid in their identification. Most of them, curiously enough, were the seeds of plants not considered myrmecochorous by Sernander, but as he points out in his monograph (p. 176), ants seem very indiscriminate in their choice of seeds, which in some cases may be used as building material. Also we must remember that many seeds which are carried by the wind (anemochorous), will be readily caught by the ant-hill, which rises above the surrounding vegetation, and will become covered up by the ants. This was probably the case with the fruits of *Anthoxanthum odoratum* (the Sweet Vernal Grass) of which twenty-seven fruits, with their awned glumes attached, were found in the portion of the nest analysed. Sernander states (p. 179) that he found twenty-two in one ant-hill of *Lasius niger* in Sweden and often saw them carrying the fruits along. On the whole however, we may, I think, attribute their presence largely to the wind. This is, I think, borne out by the fact that the fruit which was next in order of frequency was that of *Hypochæris glabra* (which is provided with a feathery pappus). Of this plant four fruits were found. I think we may probably also attribute the presence of fruits of *Arrhenatherum* (the False Oat) and *Rumex crispus* (the Dock) with fruiting perigon to the action of the wind. The seeds of *Senebiera didyma, Cotyledon umbilicus, Stellaria Holostea, Luzula campestris, Conopodium denudatum* and *Ulex europæus,* presumably owed their presence to the activity of the ants. Only one seed of each of these plants was found in the portion of the nest examined, and of these Ulex alone is considered myrmecochorous. Possibly earlier in the season the Ulex seeds might have been brought in greater quantity and then have been thrown out when the elaiosome

had been detached. But whether the seeds of Ulex are brought into the nest or not, it is obvious from the experiments detailed above, that *Formica rufa* can and does carry the seeds about.

We may therefore, I think, place the gorse and the broom in the category of plants, the seeds of which are dispersed by ants in addition to the earlier dispersal within a nearer radius, by the explosive contraction of the ripe seed pod (autochory).

The reasons for including Ulex and Sarothamnus among the myrmecochorous plants are the following :—

(1). The seeds are provided with a bright coloured caruncle containing oily food-material and resembling in structure and contents the elaiosomes of other myrmecochorous plants like *Chelidonium* (the Greater Celandine).

(2). Ants are particularly attracted by the oil-containing caruncle, and as the experiments have shown, can and will carry the seeds of the gorse about.

(3). The curious rectilinear distribution of gorse-bushes along actual or disused paths and roadways as illustrated by the instances on the Yorkshire Moor[1] and the Derbyshire plateau does not seem explicable by ordinary dispersal due to the explosive dehiscence of the dry capsule, but can be paralleled by the distribution of such plants as the Celandine along the ant-runs.[2]

Whether or not some other interesting peculiarities in the distribution of the gorse depend on the presence or absence of certain species of ants in certain localities remains still to be shown. Gèze has commented[3] on the absence of the gorse from the schists in the neighbourhood of Villefranche, while it seems to grow freely on the adjoining granites and clays, and this though topographically and climatically the same conditions obtain. Gèze is inclined to attribute this selective difference in the distribution to the fact that the schists on weathering give a very poor soil, poor even in potassium, while the granites yield a soil poor in lime and phosphoric acid, but rich in potassium. The French observer is still investigating this problem in the remarkably local distribution of the gorse, mainly from the chemical point of view ; but possibly some attention to the possible predilection of ants for one or other of the two geological formations might help to settle this interesting question.

[1] NEW PHYTOLOGIST, Vol. VII., No. 1, 1908.

[2] See Kerner and Oliver. Nat. Hist. of Plants, Vol. II,, p. 867.

[3] Gèze, J. B. Notes d'édaphisme chimique—Distribution de l'Ajonc (Ulex Europæus), aux environs de Villefranche-de-Rouergue. Bull. de la Soc. bot. de France. Tome 55, No. 6, 1908, p. 466.

THE DISTRIBUTION OF BRYOPHYTES IN THE
WOODLANDS OF SOMERSET.

By W. Watson.

THE county of Somerset has a most interesting flora, the rich-
ness of which is due to a number of causes; prominent
amongst these are the mild climate, well-wooded character, varia-
bility of rainfall, diversity of physical and geological aspects, and
last, but not least, the comparative immunity from the smoke of
manufacturing and thickly populated districts. The geology of the
county is very complicated, every system from the Old Red Sand-
stone to recent deposits being represented, giving rise to great
variability in its soils and physical geography, the peat moors and
alluvial flats of the Sedgemoor area forming a sharp contrast with
the Carboniferous limestone of the Mendips, whilst the alternation
of Jurassic clays and limestones give rise to the characteristic
undulations of the eastern portion.

The woodlands are well represented by the oak and ash-types.
In the former the oak is the dominant tree, the ash being confined
to damp situations. Oak woods, of the character of many of those
met with on the clays of the south-east of England are seldom
seen, but the oak-woods of the Upper Greensand of the eastern
boundary of Somerset are quite comparable with those on the
sandy soils of other parts of the country. The ash-woods are
dominated by the ash, the oak occupying a similar subordinate
position as the ash does in the oak-woods. The woods of the ash-
type are very variable in character, elimination of the ash and its
replacement by hazel often giving rise to a derived form of wood-
land, which is well represented in Somerset. These woods have
been called oak-hazel-woods[1], the oak and the hazel being the
dominant woody plants, while ash standards are of infrequent
occurrence. As these oak-hazel-woods are so characteristic a
feature of the county I have considered it advisable to retain the
term for local use, though they have little in common with the oak-
hazel coppices of the south-east of England, these being undoubtedly
offshoots from the lowland oak-woods. In some of the woods the
transition from the ash-type to the oak-hazel form are very striking,
recurring again and again in the course of a few miles.

[1] C. E. Moss. Geographical Distribution of Vegetation in
Somerset, Royal Geogr. Soc., 1906.

In extreme cases these three woodland associations are well differentiated, but transitions occur which are difficult to refer to any one of the types. The oak-hazel-woods are usually found at low elevations on the Triassic and Jurassic marls and clays, the oak-woods at higher elevations on the sandstones, whilst the ash-woods are especially characteristic of the slopes of the Carboniferous limestone. Dr. Moss, in his "Geographical Distribution of Vegetation in Somerset," has shown that each of these woodland types has its characteristic association of Phanerogams and Vascular Cryptogams, and I am in agreement with the general results of his careful investigations, the interesting exposition of which has earned him the thanks of Somerset botanists.

Native beech-woods are probably absent; the rings of beech trees which are so conspicuous a feature around the woods near Minehead, Taunton and Alfred's Tower have probably been planted. At Norton Fitzwarren, near Taunton, there is a small wood which almost entirely consists of beech trees, with their characteristic lack of undergrowth, but these trees also are probably planted. Extensive planting of trees has taken place, so that a large number of woods cannot be referred to any of the types; Dr. Moss refers to these as "mixed woods," an interesting case of which occurs near Yatton.

In all these woods, except where beeches are dominant, the lower forms of plant-life are abundant, bryophytes clothing the ground with a mantle of various hues, whilst the trees are draped with lichens. The commonest species[1] of the latter are *Collema flaccidum*, *Calicium hyperellum*, *Ramalina calicaris*, *R. fraxinea*, with its variety *ampliata*, *R. fastigiata*, *R. farinacea*, *R. pollinaria*, *Usnea florida*, *U. hirta*, *Evernia prunastri*, *Parmelia saxatilis* with its form *furfuracea*, *P. caperata*, *P. physodes*, *P. pulverulenta*, *P. tenella*, *Lecanora subfusca*, *L. rugosa*, *Pertusaria amara*, *P. globulifera*, *P. communis*, *P. Wulfenii*, *Lecidea canescens*, *Graphis scripta*, *Cladonia pyxidata*, *C. pungens*, *C. macilenta*, *C. pityrea*, *C. squamosa* and *Cladina sylvatica*. The lichens seem to be more susceptible than the bryophytes to the influence of man, disappearing near the towns at a more rapid rate, though *Collema cheileum* appears to be on exception to this rule.

The commonest and most prominent mosses are pleurocarpous, whilst the chief liverworts belong to the Jungermanniaceæ.

The upland ash-woods are characterised by the abundance of

[1] Names according to Crombie's Monograph of British Lichens.

saxicolous forms, the oak-woods by those bryophytes which prefer a sandy or a peaty soil, whilst in the oak-hazel-woods plants preferring a stiff soil are found. The amount of moisture present in these woods varies, but, as a rule, the oak-hazel-coppice has the greatest amount; the woods of the oak-type are of a fairly dry character, especially in upland situations, whilst the ash-woods of the uplands are the driest, those of the lower elevations approaching more closely to the oak-hazel in this respect.

The following lists are useful for comparing the different associations. The naming of the species in all cases is taken from the Census Catalogues of the Moss Exchange Club[1].

(1). The following species are abundant in all the three types of woods :—*Catharinea undulata, Dicranum scoparium, Mnium undulatum, Neckera complanata, Porotrichum alopecurum, Thuidium tamariscinum, Brachythecium rutabulum, Eurynchium striatum, Plagiothecium silvaticum, Hypnum cupressiforme* and its varieties *filiforme* and *ericetorum, Plagiochila asplenioides* and *Lophocolea cuspidata.*

(2). In the ash and oak-hazel-woods the following species, which are absent or of less frequent occurrence in the oak-woods, are found :—*Hypnum molluscum, H. cuspidatum, Eurynchium rusciforme, Camptothecium sericeum, Anomodon viticulosus, Mnium stellare, Bryum capillare* (ground form), *Encalypta streptocarpa, Fissidens viridulus* and *Radula complanata.*

(3). The following species are characteristic of the ash-woods:— *Hypnum molluscum* (dominant), *H. cuspidatum, Eurynchium striatum* (sub-dominant), *Camptothecium sericeum, Anomodon viticulosus, Mnium punctatum, M. affine, M. cuspidatum, Bryum capillare, Encalypta streptocarpa, Fissidens adiantoides* (a ground form) and *Metzgeria furcata.* In the ash-woods of the Carboniferous limestone, saxicolous species such as *Neckera crispa, Orthotrichum anomalum* var. *saxatile, Trichostomum nitidum, Ditrichum flexicaule, Grimmia apocarpa, Barbula rubella, Madotheca platyphylla* and *Frullania Tamarisci,* in addition to the above species, are common.

(4). The following species are characteristic of the oak-woods:— *Catharinea undulata* (sub-dominant), *Tetraphis pellucida, Polytrichum aloides, P. piliferum* (sub-dominant when conifers are abundant), *P. juniperinum, Dicranum majus, Orthotrichum Lyellii, Webera albicans, Mnium cuspidatum, M. hornum* (sub-dominant), *Campylopus pyriformis, C. fragilis, Leucobryum glaucum, Aulacomnium androgynum, Plagio-*

[1] The Census Catalogue of British Mosses. York, 1907.
Lett's Catalogue of British Hepatics. Eastbourne, 1904.

thecium undulatum, Hypnum Schreberi, Pellia epiphylla, Nardia scalaris, Lophozia ventricosa, Lophocolea bidentata, Kantia Sprengelii, Diplophyllum albicans, Scapania compacta and *Frullania dilatata.*

(5). The following species are characteristic of the oak-hazel woods :—*Fissidens taxifolius, F. bryoides, Mnium undulatum* (sub-dominant), *Brachythecium rutabulum* (dominant), *Eurynchium prælongum* (sub-dominant), *Webera carnea, Mnium stellare, Brachythecium rivulare, B. velutinum, Eurynchium myurum, E. rusciforme, Amblystegium filicinum, Hypnum riparium, H. commutatum, Conocephalum conicum, Lunularia cruciata, Pellia endiviæfolia, Kantia Trichomanis,* and *Radula complanata.*

Most of these species are also common in the damper ash-woods and in the woods intermediate between the ash-type and the oak-hazel form.

(6.) In the beech-woods there are comparatively few bryophytes, the chief forms being *Fissidens taxifolius, F. bryoides, Mnium undulatum, Brachythecium rutabulum, Eurynchium prælongum, Hypnum cupressiforme* with its varieties *resupinatum* and *ericetorum,* and *Frullania dilatata,* the latter being sub-dominant.

(7). The mixed woods vary to a large extent, but their bryophytes are generally similar to those of the oak-hazel association.

(8). Where pines are common in the oak-woods, the various species of *Polytrichum, Tetraphis pellucida, Leucobryum glaucum, Aulacomnium androgynum, Campylopus fragilis, C. pyriformis, Plagiothecium undulatum, Diplophyllum albicans, Nardia scalaris, Scapania ventricosa,* and *S. compacta* become more abundant.

(9). Many species which are absent or infrequent in ash and oak-hazel are common in the oak-woods.

The following list does not pretend to be a complete representation of bryophytic distribution in the woods, as so many minute species are liable to be overlooked. The plan adopted is the same as that in the "Geographical Distribution of Vegetation in Somerset," the letters in the various columns denoting the frequency, d=dominant, s=sub-dominant, a=abundant, o=occasional, r=infrequent or rare, vr=very rare, — =absent.

	Oak.	Oak Hazel.	Ash.
Sphagnum subsecundum, Nees.	o	r	—
Tetraphis pellucida, Hedw.	o	vr	vr
Catharinea undulata, W. and M.	s	a	a
Polytrichum aloides, Hedw.	a	—	—
„ *piliferum,* Schreb.	a	—	—

	Oak.	Oak Hazel.	Ash.
Polytrichum juniperinum, Willd.	a	r	r
„ *gracile*, Dicks.	o	r	r
„ *formosum*, Hedw.	o	o	o
Ceratodon purpureus, Brid.	a	o	o
Ditrichum flexicaule, Hampe.	—	vr	a
Dichodontium pellucidum, Schp.	o	—	—
Dicranella heteromalla, Schp.	a	o	o
„ *varia*, Schp.	vr	o	r
Dicranoweisia cirrata, Lindb.	o	o	o
Campylopus pyriformis, Brid.	o	vr	vr
„ *fragilis*, B. and S.	o	vr	vr
Dicranum scoparium, Hedw.	a	a	a
„ „ var. *orthophyllum*, Brid. ...	o	o	o
„ *majus*, Turn.	a	r	r
Leucobryum glaucum, Schp.	o	vr	vr
Fissidens exilis, Hedw.	r	r	—
„ *viridulus*, Wahl.	—	o	o
„ *adiantoides*, Hedw.	—	—	a
„ *bryoides*, Hedw.	o	a	o
„ „ var. *inconstans*, Schp. ...	—	o	—
„ *taxifolius*, Hedw.	o	a	o
Grimmia apocarpa, Hedw.	o	r	a
Tortula muralis, Hedw.	r	r	o
„ *lævipila*, Schwaeg....	o	o	—
Barbula rubella, Mitt.	r	r	a
„ *fallax*, Hedw.	o	o	a
„ *unguiculata*, Hedw.	r	r	o
Trichostomum crispulum, Bruch.	—	r	o
„ *nitidum*, Schp.	—	vr	o
Encalypta streptocarpa, Hedw.	r	o	o
Ulota crispa, Brid.	o	o	o
„ „ var. *intermedia*, Braithw.	o	o	o
Orthotrichum anomalum, Hedw. var. *saxatile*, Milde	r	r	o
„ *Lyellii*, Hook and Tayl.	a	o	o
„ *affine*, Schrad.	o	o	a
Aulacomnium androgynum, Schwaeg.	o	vr	vr
Webera nutans, Hedw.	o	r	vr
„ *carnea*, Schp.	—	a	—
„ *albicans*, Schp.	a	o	—
Bryum capillare, L.	o	a	a

	Oak.	Oak Hazel.	Ash.
Mnium affine, Bland	o	r	a
„ *cuspidatum*, Hedw.	a	o	a
„ *rostratum*, Schrad.	o	o	o
„ *undulatum*, L.	a	s	a
„ *hornum*, L.	s	r	a
„ *stellare*, Reich.	r	o	o
„ *punctatum*, L.	o	o	a
Neckera crispa, Hedw.	—	vr	a
„ *complanata*, Hübn....	a	a	a
Pterygophyllum lucens, Brid.	—	o	—
Porotrichum alopecurum, Mitt.	a	a	a
Anomodon viticulosus, H. and T.	r	o	a
Thuidium tamariscinum, B. and S.	a	a	a
Camptothecium sericeum, Kindb.	r	r	a
Brachythecium rutabulum, B. and S.	a	d	a
„ *rivulare*, B. and S.	—	o	o
„ *velutinum*, B. and S.	o	a	o
„ *illecebrum*, De Not.	o	—	—
„ *purum*, Dixon	a	o	o
Eurynchium piliferum, B. and S.	—	o	—
„ *crassinervum*, B. and S.	—	r	o
„ *prælongum*, Hobk.	a	s	a
„ *myosuroides*, Schp.	o	o	—
„ *myurum*, Dixon	o	o	—
„ *striatum*, B. and S.	a	a	s
„ *striatulum*, B. and S.	—	—	o
„ *rusciforme*, Milde	r	o	o
Plagiothecium elegans, Sull.	o	r	o
„ *denticulatum*, B. and S.	a	o	a
„ *silvaticum*, B. and S.	a	a	a
„ *undulatum*, B. and S.	a	vr	vr
Amblystegium serpens, B. and S.	o	o	o
„ *filicinum*, De Not.	—	o	—
Hypnum riparium, L.	—	o	—
„ *cupressiforme*, L.	a	a	a
„ „ var. *resupinatum*, Schp. ...	a	a	o
„ „ „ *filiforme*, Brid. ...	a	a	a
„ „ „ *ericetorum*, B. and S....	a	a	a
„ *commutatum*, Hedw.	—	o	—
„ *Patientiæ*, Lindb....	—	o	—

	Oak.	Oak Hazel.	Ash.
Hpynum molluscum, Hedw.	o	o	d
,, *cuspidatum*, L.	o	a	a
,, *Schreberi*, Willd.	a	o	o
Hylocomium splendens, B. and S.	a	o	o
,, *squarrosum*, B. and S.	a	o	o
,, *triquetrum*, B. and S....	a	a	a
Conocephalum conicum, (L.), Dum....	r	a	r
Lunularia cruciata, (L.), Dum.	r	a	r
Metzgeria furcata, (L.), Lindb.	o	o	a
Pellia epiphylla, (L.), Dum.	o	r	r
,, *endiviæfolia*, (Dicks), Dum....	r	a	o
Nardia scalaris, (Schrad.), Gray	a	r	r
Lophozia turbinata, (Raddi.), Steph.	—	o	—
,, *ventricosa*, (Dicks), Dum.	o	vr	vr
Plagiochila asplenioides, (L.), Dum.	a	a	a
Lophocolea bidentata, (L.), Dum.	o	r	r
,, *cuspidata*, Limpr.	a	a	a
,, ,, var. *alata*, Mitt.	—	o	—
,, *heterophylla*, (Schrad.), Dum.... ...	o	—	—
,, ,, var. *laxior*, Nees. ...	o	—	—
Saccogyna viticulosa, (Sm.), Dum....	—	o	o
Cephalozia bicuspidata, (L.), Dum....	a	a	a
Kantia Trichomanis, (L), Gray	o	a	—
,, *Sprengelii*, (Mart.), Pears.	a	o	—
Trichocolea tomentella, (Ehrh.), Dum.	—	o	—
Diplophyllum albicans, (L.), Dum....	a	r	r
Scapania compacta, (Roth.), Dum....	o	vr	vr
Radula complanata, (L.), Dum.	r	o	o
Madotheca platyphylla, (L.), Dum....	r	r	a
Frullania Tamarisci, (L.), Dum.	—	—	o
,, *dilitata*, (L.), Dum.	o	o	o
Lejeunea cavifolia, (Ehrh.), Lindb....	—	—	o

For some suggestions as to the relations between the different forms of woodland I am indebted to Mr. Tansley, whilst Mr. Ingham, the Secretary of the Moss Exchange Club, has kindly helped me in the determination of many of the species.

THE BOUCHE D' ERQUY IN 1908.

[Text-Figs. 3—5].

OBSERVATIONS on this Breton salt-marsh were continued during last year, when two minor visits were paid, in the spring and autumn respectively. Unfortunately, it was impossible to organize the usual annual expedition on the large scale, so that no great amount of work was accomplished in the autumn.

Judging from local reports, the summer of 1908 was particularly bad at Erquy as regards its weather. The total amount of rain was not large,[1] but there were some fairly heavy downpours. For example, on May 14th there was half an inch of rain, on June 1st and 2nd more than one-and-a-half inches fell, while on July 12th and 13th a little less than one inch was measured. On the other hand there were many rainless periods; thus, no measurable quantity of rain fell from July 28th to August 20th. As regards other climatic features the weather was cold and particularly windy from about the end of June.

An examination of the area in September showed that the vegetation presented a greater differentiation as regards colour than in the previous year; thus the " crimson plain " was more crimson than in 1907, though perhaps hardly so bright as in 1904.[2] Again, the "apple-green" *Salicornia* was really bright in colour, very distinct and much more abundant than in 1907. This was especially the case in the depressions and in the fringe of the *Juncus* formations. In some places the "apple-green" *Salicornia* was so abundant as to form a turf, the general appearance being that of a fine compact growth of stonecrop. As regards size the characteristic plants were stunted, especially in exposed situations; in more protected places (*e.g.*, local depressions, etc.), they were of better growth and taller. The cupressoid form of *Salicornia* was much more abundant than in previous years. All the grass (*Glyceria maritima*) was poor and brown in colour.

Marsh-Building.

In the last report (New Phyt., Nov., 1907, p. 244), the more salient features of the processes concerned were given, and attention

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[1] From April to August, inclusive, 6·13 inches fell on the Bouche.

[2] See Report in New Phytologist, Vol. VI., p. 245, 1907.

was drawn to the extension of the vegetation in various directions, especially to the extension of the area of vegetation under the dunes (Fig. 3, A and B).

A detailed map was made of the apex of this advancing vegetation in the autumn of 1907, in order that the progress of colonisation
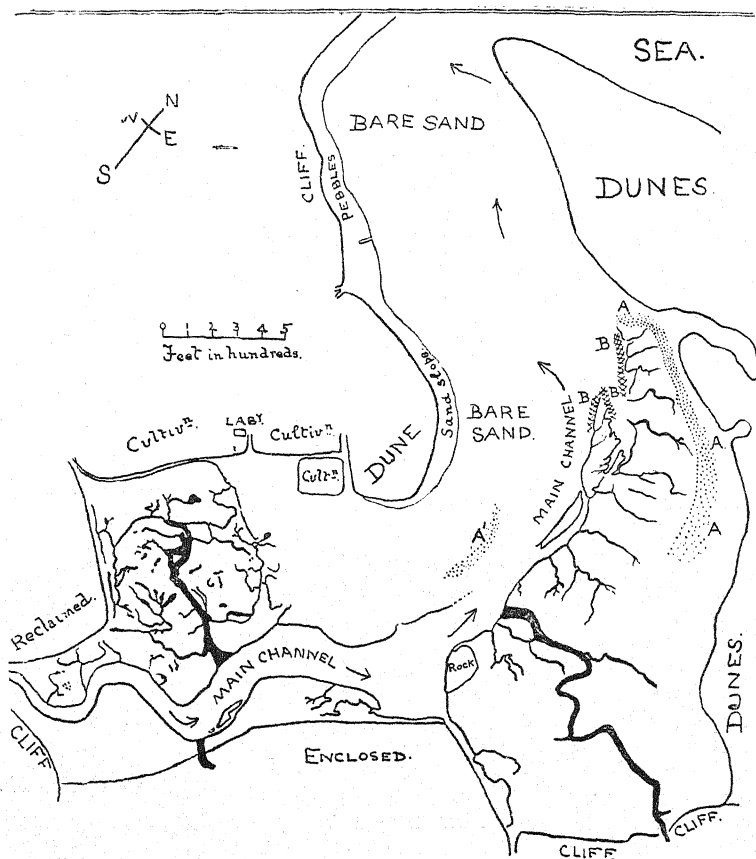
Fig. 3. Sketch map of the Bouche d' Erquy shewing the complex system of natural irrigation-channels by which the tide gains access to the marsh. The plant-associations are not represented. The areas adjacent to the two principal channels (heavy black) consist of established turf, whilst the region on the right, running up to the dunes, corresponds to an earlier phase of development. The shading at A—A and A¹ marks the pioneer zones of *Salicornia radicans*, whilst at B—B (cross-hatching) *Salicornia ramosissima* plays an analogous rôle. The banks of the main channel are not drawn in its lower part, but its course is indicated by arrows. Scale 1/8750.

could be kept under close observation. A careful comparison was made this last autumn, when it was found that a marked advance had taken place. On the north-western face, the vegetation had advanced about forty feet on previously uncolonised sand, the

advancing plants being *Salicornia radicans*, which were fairly numerous and of a medium size, and small plants of *Suæda maritima*, much scattered and fewer in number as compared with the *Salicornia radicans*; the plants of *Suæda* became more numerous towards the dunes.

On the north-eastern flank—*i.e.*, the side towards the dunes—the advance was even more marked, and the pioneer plants occurred in two zones: abutting directly upon the pre-existing vegetation, was a curved area consisting of a fairly close formation of *Salicornia radicans* and *Suæda maritima*, projecting twenty feet from last year's front; while beyond this there was an additional zone, where the soil is much looser, having a maximum width of sixty feet, and covered very sparsely with the same plants, of which *Salicornia radicans* was very small indeed, in fact not much advanced beyond the seedling stage. Also, the vegetation of the eastern flank had made much progress towards the dunes (Fig. 3, A).

As regards other parts of the Bouche, there has been much colonisation of the sand on the side of the old dune (Fig. 3, A, in the centre) in a south-easterly direction. The chief plants noted in this advance were a fescue, together with *Euphorbia Paralias*, *Hieracium* sp., and *Eryngium*. Further, it was noted that the *Obione* patches in line with the "Council" Rock were distinctly larger and extending over a larger area.

With regard to the formation of hummocks and the part played by *Salicornia radicans*, attention has already been drawn (NEW PHYT., 1907, p. 250). The locality mapped in the spring of 1907 was re-charted in September, 1908, and a comparison of the two (Figs. 4 and 5) shows that the advance has been maintained. The size of the hummocks has considerably increased, and much coalescence of previously isolated hummocks has taken place. Further, a few new hummocks have come into being, and also new plants of *Salicornia radicans* orientated transversely to the stream. On the other hand, many of the old hummocks have lost their patches of *Salicornia radicans*, and are covered entirely by a turf of *Glyceria* and *Suæda*.

TRANSPLANTATIONS.

In the Autumn of 1907, two bare patches of sand, one in the bed of stream B and the other on a low sand-bank in the main river opposite the mouth of stream B, were planted with *Salicornia radicans*. The examination of these inoculations last September

shewed that the first was unsuccessful, for no hummocks were
formed and the plants were practically obliterated : in the second
case, the Salicornias planted in the main stream held their own,
some were ranged at right angles to the course of the current and
had accretions of sand around them.
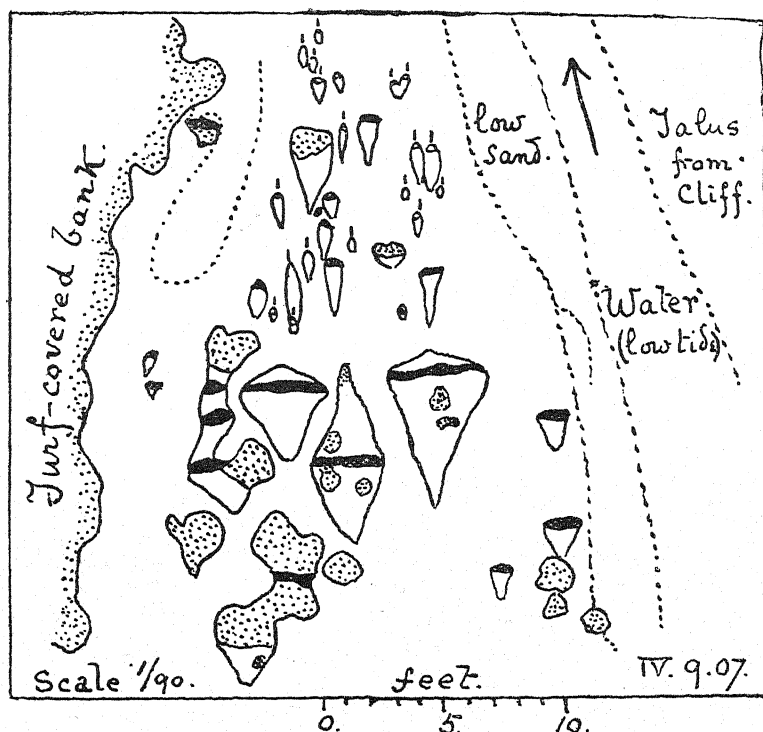
Fig. 4.   Map (charted April, 1907) shewing colonisation of a sand-bank in
the bed of a channel.   The rhomboidal figures are the outlines of sand
hummocks collected since 1903 by plants of *Salicornia radicans* and *S. herbacea.*
The black transverse belts mark the *S. radicans,* whilst the position of *S herbacea*
is marked by short vertical strokes.   The hummocks accumulated by the
latter are relatively small.   The shading marks areas (hummocks) further
colonised by *Glyceria maritima* and *Suæda maritima.*   These two plants do not
appear to settle directly on the sand-bank itself.   The arrow points down
stream.   Scale $\frac{1}{90}$.

During the course of the past year considerable interest has
been aroused through the publication by Dr. Stapf of some account
of the part played by forms of *Spartina* in the colonization of mud
in Southampton Water and the Solent.   It would appear that
S. alterniflora and especially a supposed natural hybrid between
this species and *S. stricta,* known as *S. Townsendii,* have been
rapidly advancing along these shores in recent years and exerting a

very striking change by consolidating and raising the bare mud-flats.[1] Under the circumstances it was decided to experiment with *Spartina* at Erquy (where none of the forms occur) with two objects in view : (i.), to study its behaviour in a sandy marsh, (ii.), by the concurrence of the two parent species to see whether the supposed hybrid, *S. Townsendii*, would appear spontaneously.
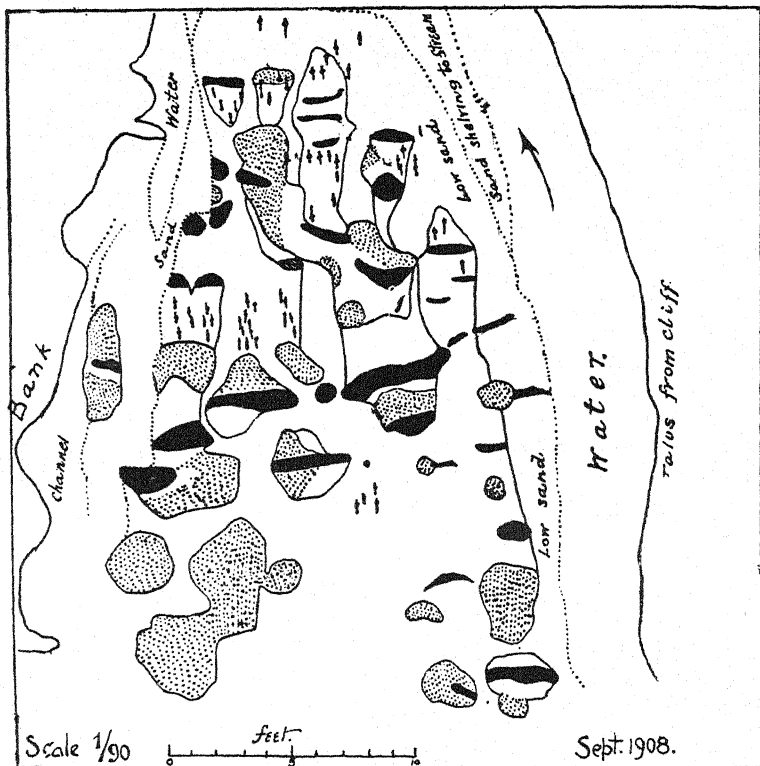
Fig. 5. The same sand-bank re-charted in September, 1908, shewing advance in colonisation. Explanation and scale as in Fig. 4. The greater breadth of the transverse belts of *S. radicans*, as compared with those in Fig. 4, is due to the difference in the seasons when the charts were made.

On the occasion of the April visit, with the co-operation of Dr. Stapf, rhizomes of *S. alterniflora* were obtained at Southampton and transplanted into the muddiest ground available at Erquy, it being the intention, should the plant become established, of intro-ducing *S. stricta* later on from a locality about twenty miles away. The experiment, however, would appear to have failed, as no traces of *S. alterniflora* were to be discovered when the spots were examined in September.

[1] O. Stapf. *Spartina Townsendii*. Gard. Chron., 1908, p. 33.

In connection with this part of the report it may be mentioned that at the invitation of the Royal Commission on Coast Erosion and Land Reclamation, evidence largely based on the Erquy work was given last spring by Professor Oliver on the part played by the halophytes as sand and mud binders, whilst Dr. Stapf gave information arising out of his observations on the Spartinas in the South Hampshire area.

OTHER OBSERVATIONS.

During a visit in November, 1907, the seeds of typical apple-green and crimson examples of *Salicornia herbacea* were harvested from numerous localities on the marsh. The following April these were sown on small denuded areas, ranged together so that the crops could be readily compared. The conditions thus obtained were not identical in detail with those ruling in the several parent-localities, but approximate uniformity of growth-conditions was secured in a halophytic environment.

When examined in September, 1908, the results on the whole were found to be meagre, as only a small proportion of the seeds sown were represented by the standing crops. Of the twelve original batches sown (six green and six red), three of each sort were represented in sufficient numbers for a conclusion to be drawn. Stated quite broadly the result, which has been confirmed by various other observations, was that the parental colour was transmitted, *i.e.*, seed from crimson parents produced crimson or reddish offspring, that from green parents green offspring. On the whole the red offspring gave a somewhat more decisive result than the green, as the former were more numerously represented.

These and other experiments point to the conclusion that the colouration of these plants is a more complex phenomenon than is sometimes supposed. The problem is one that should be attacked on the large scale by extensive sowings under controlled conditions including, if possible, controlled pollination.

These and previous experiments involving the sowing of seeds on the marsh show that the technical difficulties involved are considerable and that they can only be overcome by taking special precautions in connection with the following points. Under natural conditions the seed of the annual Salicornias and Suædas drops from the parent plant in November and germinates in the early spring. The process of germination is evidently promoted by the rich surface-growths of the alga *Rhizoclonium* which spread over them and act as a wet mulch. Whilst the surface algæ exert a

marked influence in fixing the seed and protecting the embryos at the time of establishment, observations on migration prove that a proportion of the seed is transported from place to place—no doubt by the tides. For if an area be denuded of every plant of *Salicornia* long before the seed is ripe, a fresh crop of *Salicornia* will appear upon it in the spring, although it may have been demonstrated by control washings of samples of the soil that the amount of dormant seed in the soil persisting from a former year is a negligeable one.

By harvesting the seed in November and sowing it at the beginning of April on areas that have been denuded immediately before the sowing, the danger of contamination is no doubt reduced to a minimum, but the resulting crop is always meagre because the process of denuding and preparing the ground involves interference with the important *Rhizoclonium* covering. Thus while Scylla is evaded we become involved in Charybdis.

If therefore the cultivations must be carried out on the marsh, and there are strong reasons why they should be, it would seem that the experimental patches should be protected during the critical period from invasion by water-carried seeds. To ensure the effective enforcement of this precaution expert supervision is essential during the winter months—supervision which can only be exerted by residence in the sphere of operations.

During the spring of 1908 a series of preliminary experiments on the osmotic phenomena of the root-hairs of *Salicornia* and *Suæda* seedlings were concluded. The results, which have already appeared in these pages,[1] show (i.) that the root-hairs of plants growing in places where the soil-water is strongly saline can accommodate their internal osmotic pressure as the salinity of the water of the environment falls in concentration; (ii.) that they also have the capacity of raising their internal osmotic strength in proportion to the increase of the external salinity.

A number of readings with the wet and dry bulb thermometer were taken at various heights at different stations with a view to investigating the vertical distribution of humidity.

Photographs were taken in the autumn from many of the viewpoints of former years so that there should be no break in the continuity of the records of changes in the vegetation.

<div align="right">T. G. HILL.</div>

[1] T. G. Hill. Observations on the Osmotic Properties of the Root-Hairs of Certain Salt Marsh Plants. NEW PHYTOLOGIST, Vol. VII., p. 133.

DISCUSSION ON "ALTERNATION OF GENERATIONS"
AT THE LINNEAN SOCIETY.

THE Meeting of the Linnean Society of London on February 18th, 1909, was devoted to a discussion on this subject, following a paper by Dr. W. H. Lang. A general desire was expressed that the paper and discussion should be reported *in extenso* in the NEW PHYTOLOGIST. The paper and most of the speeches which followed are reported practically *verbatim* as they were delivered, but Professor Bower and Professor Farmer preferred to supply their own versions. The Editor is much indebted to Miss Agnes Robertson, who kindly took careful and very accurate notes of the speeches. The reports based on these notes have been revised by the speakers for publication.

Dr. Lang spoke as follows :—

I should like in the first place to acknowledge in a word my sense of the honour of being invited to contribute this opening paper to the discussion to-night, and, as time is limited, shall address myself at once to my subject.

We are all clear as to what we understand by the well marked alternation of generations in the life-history of a Fern or a Liverwort. I shall confine my remarks to points bearing on the origin of alternation of this type, and not enter into the wider general question of the origin of alternation of generations at large. Time will not permit of summarising the diverse views held on the subject, but these will be better dealt with by others in the course of the discussion.

Not only are the sexual and spore-bearing generations clearly different in form in archegoniate plants, but there is a constant cytological difference between them. The cells of the spore-bearing or diploid generation have nuclei with twice the number of chromosomes of those forming the sexual or haploid generation. In certain Algæ such as *Dictyota* we find a corresponding alternation of sexual and spore-bearing individuals with the same cytological difference.

Alternation of generations presents us with a problem in ontogeny as well as in phylogeny, and it is possible that the phylogenetic problem may be best attacked through the ontogenetic. I shall ask you to consider briefly how we are to look on the ontogeny of an organism with two alternating generations in its life-cycle; this appears to present difficulties that have hitherto not been fully faced. It is more complicated than the ontogeny of an organism without alternation. In this we can look on the germ-cell giving rise to the individual as a specific cell, the nature of which, under the usual conditions, determines the result. Each cell of the individual would correspond to the specific cell and any cell of the body would therefore be theoretically capable of reproducing the organism. We may regard the production of the individual from the germ-cell as due partly to the external conditions and partly to internal correlations and the mutual influence of the tissues.

In the life-cycle of a plant with definite alternation of generations we meet twice with a germ-cell capable of giving rise

[The slides shown included photographs of the haploid and diploid individuals in *Dictyota* and *Polysiphonia*; *Coleochæte*, the fruit-body of which it was suggested might be regarded as a mass of haploid cells, influenced by retention to simulate a sporogonium; *Oedogonium*, with no second generation but the division of the zygote into four zoospores; Bryophyta, in which the influence of the enclosing generation lasts throughout the development of the sporogonium; apospory in Mosses and in *Anthoceros*, in which cells of the sporophyte more or less isolated from their connections and placed under the conditions of a germinating spore, behave in their further growth like the latter.

In Vascular Cryptogams the retention of the spore-bearing in the enclosing sexual generation ceases after a time, but not until the main organs of the plant have been laid down, and a state of formative induction of the already formed parts on the future development may be supposed to be established. Examples of the great phyla were considered, and it was suggested that the leaves of Lycopods and *Equisetum* might correspond to the lobes borne on the prothallus, while in the Ferns the comparison was rather between the early leaves and a whole branch of the prothallus. Correspondences between the sporangia and the antheridia in the various groups were also indicated. The protocorm of *Lycopodium cernuum* and other species, while not necessarily a primitive organ, was considered an expression of the capacity of the diploid embryo, brought partly under the conditions of life of the prothallus, to take on resemblances to the latter.

The remarkable body of evidence which the facts of apospory and apogamy supplied by the Ferns was briefly reviewed. Though apospory and apogamy probably represent nothing that has formed a stage in descent, they afford valuable data as to the causes of the ontogeny.]

I have avoided till now entering into the bearing of the different conditions of ontogenetic development of the two generations in the life-history upon the antithetic and homologous theories of alternation. I do not intend to do so fully now; time is limited, and this will be done better by other speakers. I would point out, however, that the facts we have learnt in recent years, as to the nuclear difference between the two generations in archegoniate plants and in certain Algæ, have tended to modify both the great rival hypotheses and made it more difficult to define their essential characteristics. This is a subject upon which the discussion may throw more light.

From one point of view an alternation such as is seen in *Dictyota* may be regarded as antithetic, and from another as homologous. We have an antithesis in cytological characters, but such an agreement in the organisation of the two generations that I should regard them as homologous. This plant also suggests that the diploid generation need not in any way have been the result of *gradual interpolation* and *progressive sterilisation*, which may be regarded historically as the central idea of the antithetic theory. On the other hand I do not see any evidence for the spore-bearing form being the result of gradual modification of a sexual individual, which may be taken as the main idea of the older homologous theory. I see no reason why, if reduction did not take place in the zygote, we might not get *suddenly* from the latter, a generation

resembling in form and organisation the sexual one, but with diploid cells and reproducing by spores formed after a reduction division. Such cases as *Dictyota* and *Polysiphonia* are the new wine that threatens to burst both the antithetic and homologous wine-skins as originally sewn up by Celakovsky and Pringsheim.

I do not venture to anticipate what may be an ultimate complete explanation of alternation of generations. Nor do I wish to put out of account the possibility of the different states of the specific cell being shown to have some causal influence on the differences of the resulting individuals in archegoniate plants. In stating this ontogenetic hypothesis before you, I am not concerned altogether with its truth. It is an attempt to look at the question in the light of the new, if imperfect, facts before us. The value of such an hypothesis lies in its use as a working tool, more than in its truth. I am in the position of a surgeon exhibiting a new instrument, with which he has never performed a major operation, but which he hopes may prove of use in his own hands or in those of more skilful colleagues. This working hypothesis may be of use in directing to new lines of enquiry and experiment, some of which may test the hypothesis and support or disprove it. The critical experiment would be to get, *e.g.*, the fertilised egg of a fern to develop free, under the conditions that usually act on the spore. On my view it should give rise to an individual with the form and organisation of the prothallus. The converse experiment, of placing the spore under the conditions of the zygote, is less practicable. Such experiments are wanting, but some of the facts ascertained regarding induced apogamy and apospory appear to approximate to these results.

Professor Bower, who opened the discussion, said that it might have been reasonably expected that after so important a communication as that by Dr. Lang, the President should speak first; but he thanked the President for permitting him to follow Dr. Lang, so that he might give some explanation of the bearing of the views now submitted upon the position of those who had upheld the antithetic theory in its old form : this would clear the ground, and make plainer the issues as they would now stand. He hastened at once to admit the cogency of the ontogenetic view now propounded ; but the position of Dr. Lang appeared to him to be that of presenting a new aspect of certain most important facts relating to alternation, rather than in itself a new theory. Dr. Lang did not probe into the ultimate origin of the two phases of the life-cycle, but dealt with them as already established, leaving the question of the ultimate origin of the generations very much where it was. What the new ontogenetic view did do was to modify very profoundly the aspect of the sporophyte in the two series of the Archegoniatæ : under the old antithetic theory the sporophyte was assumed to have been dependent *ab initio* ; its dependence would not now be held to be primary, but secondary, and we should contemplate the encapsulation of a generation originally free. If this were accepted, then the great bugbear of those who held by homologous alternation in the past, (*viz.* the origin of the whole archegoniate sporophyte from a body primitively fertile throughout, by a process of sterilisation) would fall away, for the subsumed generation might have been already provided with both sterile and

fertile tracts. Sterilisation, in any case an important factor, would take its place as not necessarily involved in the first steps of development of the Archegoniate sporophyte. A consequence of this would be to shunt the Bryophytes from their position as a key to the origin of the sporophyte : there would not be felt the same tendency or perhaps need, as heretofore, to hold them to be phyletically isolated. The two great series of the Archegoniatæ would rather present parallel problems of encapsulation, which event might have occurred independently in the two series, and the one would not necessarily elucidate the other. Thus Dr. Lang's suggestion would act as harmonising some of the differences which existed between the adherents of the two old theories.

A further effect would be to shift the focus of enquiry from the Archegoniatæ to the Algæ, so far as ultimate origin of alternation was concerned. Dr. Lang had remarked that indications were wanting among Algæ, such as *Dictyota*, that the sporophyte had had any history of gradual interpolation. He (Professor Bower) would wish to point out that indications of any other mode in them were equally wanting. At the present moment we were in a condition of ignorance on that question, which was quite charming. One important effect of Dr. Lang's paper would be to direct attention to the study of the Algæ, and more especially to their cytological cycle : this had to be examined in relation to their external form. And here it might be remarked that it was unfortunate that hitherto attention had been devoted mainly to advanced forms, such as *Dictyota* and *Polysiphonia*; it was rather from the comparison of simpler forms that evidence as to how the alternating generations originated might be anticipated.

It might be thought from all this that the old antithetic theory was gone beyond repair. He did not think that it was. We still had each normally completed nuclear cycle presenting two main events— zygote-formation and spore-formation, with the doubling and reduction of chromosomes ; he was disposed to hold that the phases intervening between these two events had been phyletically distinct throughout. It might be said that this was not the old antithetic theory, and of course it was not, for the whole cytological story had been revealed since the discussion of alternations arose ; but the two intervening phases corresponded in essentials to the phases of the antithetic cycle. A further question which now presented itself was this :—if these two phases were phyletically distinct throughout their history how far could the parts produced upon them respectively be held to be comparable, or be designused as " homologous " ? Unfortunately the word homologous grees of with very different significations; there were different cal phyletic homology, the most stringent being that of ideres of the two history. It need not be surprising that appendaey did in certain generations should resemble one another, as basis; but he would cases, being produced from a similar plasmant had the the same not regard them as having on that accc the old idea of the his- phyletic history; he would wish to retaiting phases ; he did not, in torical distinctness of the two alterfull morphogenetic unity of the fact, feel prepared to concede the

spore and the zygote. ach a position was contrary to the It might be said that Digby, and those of Strasburger, who had results of Farmer and Miss me-number did not necessarily determine shown that the chromos

9.15 form: but it should be carefully considered whether the possibilities of chromosome behaviour as seen now illustrated precisely what had happened in the past; whether the variations from the normal cycle alluded to were not *ex post facto* occurrences; they were not normal or even usual occurrences now, and it might be questioned whether they really repeated actual history. The normal cycle seemed to him the phenomenon with which we had mainly to do in all discussions on the origin of alternations; if this were kept clearly in view tne historical distinctness of the two generations, even where their form was most alike, seemed naturally to follow.

The President, Dr. D. H. Scott, said that he agreed very cordially with all that the last speaker had said in his general remarks on Dr. Lang's theory. The first point he would like to make clear was that, in his opinion, Dr. Lang's theory did not supersede the old views; it no more superseded the homologous theory than natural selection superseded evolution. So far from superseding the homologous theory the new hypothesis owed its point to the assumption that that theory was true. Dr. Lang's theory was valuable just in so far as it helped to explain the great difference between the two generations, a difference which was the obvious difficulty when they were regarded as homologous. These differences were no difficulty on the antithetic or intercalation theory—the sporophyte being a new structure there was no reason why it should resemble the other and older generation. But when the two generations were regarded as being ultimately derived from similar individuals then the existing difference between them was the point to be explained; Dr. Lang's working hypothesis as to the origin of alternation as it occurred in the higher plants, assumed, to use his own words, (NEW PHYT., Vol. VIII., p. 8,) that the archegoniate plants had arisen " from forms in which a sexual (haploid) and asexual (diploid) generation of similar form alternated regularly." This was precisely the homologous doctrine in so many words, as it had taken shape in their minds since the discovery of the cytological facts in *Dictyota*. These discoveries had shown that cytological differences did not preclude the two generations being homologous, and had thus completely removed the value of the cytological distinction as supporting the antithetic theory. For in the Dictyotaceæ we had two generations, one with the double, and the other with the single chromosome number, bearing spores and sexual cells respectively, and yet the two generations corresponded perfectly, as perfectly as Pringsheim could have desired. They owed a great debt to Pringsheim in this matter. He had laid stress on the almost absolute severance between the sexual and asexual individuals in certain Thallophyta and their consequent, more or less regular succession,[1] though no such good cases as had now been found in the Dictyotaceæ and also in the Florideæ were known to him.

Dr. Lang's leading idea was that the great difference between the two generations was to be explained by the enclosure of the egg in the maternal body, while the spore developed free. To sub-stantiate this idea it had to be shown that enclosure in the body of the parent actually produced a great effect in the right direction in analogous cases. Dr. Lang had mentioned the case of the

[1] Gesammelte Abhandlungen, Bd. II., p. 388.

Florideæ; the speaker would like to call attention to the effect of
germination of spores within the sporangium, as observed by Mr.
Boodle in *Todea*. This change of conditions led to a precocious
formation of reproductive organs, while the rest of the body was
much reduced; similarly in the spore-bearing generation of *Riccia* we
had precocious spore-formation and complete reduction of all vegeta-
tive parts, except the epidermis of the spore-sac. To a certain extent
the comparison might be extended to the Bryophytes generally, but
the analogy did not help us much with the Pteridophytes. In
Gymnosperms the female prothallus was retained in the mother
plant, while it was free in the heterosporous Pteridophytes, but the
retention did not seem to have had much effect on the prothallus,
compared, for instance, with that of such a form as *Selaginella*. In
the Angiosperms on the other hand, retention of the megaspore
appeared to have produced a great effect on the prothallus, but
entirely in the direction of reduction. It seemed a little doubtful if
there was anything in the retention of the specific cell to account
for the enormous elaboration of the sporophyte of the higher plants.
The new view (like the old antithetic theory) seemed to fit the
Bryophytes better than the Pteridophytes. He would be inclined
to think that the ancestors of the Pteridophytes already had both
generations somewhat highly differentiated, and if so, reduction in
the gametophyte might have played almost as great a part as
elaboration of the sporophyte in the differentiation of the two
generations. There was no direct evidence on this question, the
fossil record did not go far enough back, but the reduction of the
gametophyte was clearly coupled with land life, for the generation
that was bound down to semi-aquatic conditions, would have found
its development cramped. These considerations were perhaps of
some little importance in comparing the two generations of the
same plant, a comparison of which one wondered that more had
not been made before. He supposed the reason was the independent
modification of the two generations, which had obscured the original
common characters, so that great difficulties were placed in the
way of such comparison.

One of the most interesting things in Dr. Lang's paper was the
comparison of early stages in the development of the prothallus and
of the sporophyte, especially in the remarkable cases of apogamy
and apospory. He was not quite clear about one point in the
comparison, namely as regarded the Equisetaceæ. He himself
used to place the Equisetaceæ with the Lycopods as primitively
microphyllous plants. Now he had come to the conclusion
9.30 that the former were more probably derived from large-leaved
forms. Dr. Lang's illustration of the prothallus, with its
relatively large lobes, did not seem to favour the view that the
Equiseta were primitively microphyllous, though he gathered that
Dr. Lang still placed them with the Lycopods as essentially
microphyllous forms.

The main thing, from the speaker's point of view, was that the
most serious theoretical difference which had divided Professor
Bower and his school from some of them, seemed to have now
practically disappeared. He understood that the doctrine of an
intercalated generation was no longer applied to the Archegoniate
plants; intercalation was relegated to some point in the evolution
of the Algæ, and perhaps not very strongly insisted on even there.
The speaker was not an algologist, and was well content with the

present position of the question as it affected the higher plants, in which his chief interest lay.

Professor Farmer remarked that in spite of what had been put forward, he still appeared as an entirely unrepentant and unre-generate sinner so far as his attitude towards the alternation of generations was concerned. He desired to pay a tribute of admiration to the work of Lang and of Schenck, as having served to concentrate attention on new and suggestive points of view. But he did not believe that any insight was afforded thereby into the causes which *in the first instance* were responsible for the cyclical alternation, nor did he think that the rival claims of the homologous and antithetic theories were capable of being decided on such lines. The matter was one of actual history, but the difficulty was that we could neither ascertain directly how the real course of events proceeded, nor could we, in attempting to recon-struct them, agree as to the criteria which might be decisive. Much had been made of cytological criteria. The common association of the haploid condition with the gametophyte, and of the diploid with the sporophyte had appealed to many as indicating a causal nexus, and so long as the coincidence was without exception those who urged *post hoc ergo propter hoc*, occupied a strong position. But it was evident that this reliance upon a supposed *physiological cause* was bound at once to prove illusory, on the discovery of the first well-founded exception. The facts of apospory and apogamy, as soon as their cytological features were cleared up, shewed that, regarded as a cause, neither of the cyclical nuclear changes involved in fertilisation and in meiosis respectively, could any longer be regarded as necessarily, or causally, related to those other cyclically occurring morphological changes in plants which exhibit alternation of generations. The two events were cyclical, and they might be coincident, but more than this could hardly be seriously urged, especially when the fact was remembered that the nuclear processes in question were not only of general occurrence in the higher animals and plants and the processes by which they were respectively brought about were similar in these widely diverse organisms, but that they occurred just the same, even when alternation of generations was either lacking altogether or was associated with other points in the life-history.

It seemed quite probable that alternation might differ in character in different phyla, whether it was homologous or antithetic. That it was intercalated was a question that must be decided on grounds other than cytological.

The case of *Dictyota* had already been mentioned by others, but it seemed to gather in interest if taken together with *Fucus*— always a puzzle to the alternationists. The speaker would be quite prepared to admit the probability of homologous alternation in *Dictyota* (although not perhaps for the same reasons that had been urged by others), and especially when it was regarded in connection with *Fucus*. In the latter plant, the so-called oogonium first existed as a diploid cell. The oogonial nucleus then passed through meiosis, and the four resulting nuclei lying free in the protoplasm, waited for some time before undergoing the final division whereby the eggs were produced. The oogonium was thus a " tetra-sporangium " first, owing to the onset of meiosis in the sexual cycle at this particular stage. In *Dictyota* we had the *escape* of the

tetraspores, which only after independent life and cell-multiplication gave rise to the eggs which in *Fucus* were produced in the same receptacle as the tetraspore. The tetrasporangia might be looked upon, in this group, as real homologues of the oogonia, a comparison which was supported by the similarity of the tetraspores to the oospheres, which shewed such capacity for parthenogenetic development, recalling in this respect what occurred in still less stereotyped Phæophyceæ. Although a case for antithetic alternation might with consistency be made out, alternation in this group seemed to have had a different *historical* origin, and to have entirely lacked features which were present in plants exhibiting what appeared to some to be evidence for antithetic alternation.

In the *Polysiphoniæ* there seemed to be other reasons for regarding the carposporic organism as representing an intercalated (antithetic) phase, and a series shewing increased complexity of structure might be readily traced in this phylum from the simpler to the more advanced forms. But the confusion introduced by the illegitimate use of meiosis had obscured the meaning of historical events, as elucidated by morphological comparison, and led to the unwarranted assumption that the *tetraspore* marked the limit between the intercalated new, and the older generation. So far as we had any evidence, meiosis itself seemed to have coincided with the formation of *carpospores* in the lower members of the Florideæ, and the resulting plant propagated itself vegetatively, *i.e.*, within the limits of the one generation, by monospores. It seemed not impossible that these were the forerunners of tetrasporangia, by the shifting of meiosis on to them in the more advanced types. The inter-

9.45 calated phase, the carposporic plant, might well owe its peculiarities of form to its nutritional dependence on the parent plant, as Dr. Lang suggested, but this did not touch the conception we might form of it as representing a new, intercalated, antithetic, phase in the life-history.

Again as regarded *Coleochæte*; Allen's discovery that meiosis occurred, not at the formation of zoospores, but at the first division of the zygote, seemed to have settled, for some people, the intra-oogonial plantlet as representing an example of an homologous alternation. General consideration of the relations of meiosis indicated that this was a *non sequitur*. The real point to be decided was not the point in the life-history at which reduction occurred, but whether the intra-oogonial phase could be regarded as the actual descendant of a real *Coleochæete* plant, modified indeed by its retention within the oogonium, but phylogenetically identical with the free-living form; or whether the stages intervening between the formation of the zygote and the liberation of the zoospores did not represent a new and additional phase intercalated in the life-cycle. If this were conceded it would appear to be difficult to escape the conclusion that we had in *Coleochæte* not only a fine example of alternation of generation in the antithetic sense, but also an instance of the independence of this condition and that of the meiotic phase.

The Archegoniatæ, again, had to be discussed on their own merits. It would seem almost impossible seriously to urge that the Bryophytic sporogonium was anything but an intercalated stage in the life-history, and that, in the strictest sense of the words, it represented an example of antithetic alternation. It would require a high flight of imagination to explain how the gametophyte, by any conceivable series of modifications actually occurring as historical

events during descent, could have given rise to the sporogonium. Thus, whether we chose to regard *Riccia* as a starting point or not, most people would admit that the sporogonium in the Bryophyta had from the first developed on its own lines, from the zygote : that it had not arisen by modification of a pre-existing organisation, but had achieved its present complexity as the result of an intercalated cellular development, which had from the first been outside the track followed by the gametophyte—the latter track being only resumed on the germination of the spores.

As regarded the Vascular Cryptogams, the problem had again to be faced, and faced independently of any conclusions at which we might arrive respecting the lower forms of plants. Once more the matter was one which could only be settled by appeal to historical probability, based on comparative morphology. And although the evidence might not be so clear as in some of the other phyla, the speaker was led to adhere to the antithetic theory, because it appeared to be that most easily reconcilable with the facts as we knew them. It was difficult to believe that a prothallium ever again arose as the direct outcome of the zygote, led a parasitic life upon its predecessor, and then evolved an independent existence as a " sporophyte " with all the potentialities of development which we saw realised around us. The initial step, that of parasitism, was not one which, so far as we knew, would be likely to lead to such a condition. Parasitism in a form *already elaborated*, tended to effect reduction, not amplification, of vegetative parts, and we saw as a matter of fact that parasitic dependence on the *sporophyte* had culminated in remarkable reduction in the organisation of the once free-living gametophyte.

Comparisons had been made between similarities existing, especially under certain conditions, between the sporophyte and gametophyte of ferns and other Vascular Cryptogams. These resemblances might, however, be regarded as examples of homoplasy rather than of homology.

Professor F. W. Oliver said that he thought Dr. Lang had in his opening address, gone a long way to establish the homologous theory on a firmer basis than it ever had before by showing how the linked generations might come to have the relations they actually had. There was much to be said in support of the view that the archegonium originally liberated numerous gametes—as the antheridium did still—and that the passage to terrestrial life with the concomitant difficulty of launching these bodies, might have led to reduction in numbers of the effective gametes, absence of dehiscence and retention, in other words, to the evolution of the archegonium as they knew it. In the case of the seed-plants they had a converse process. So far as any morphological conclusion could be regarded with confidence, they might take it that the female gametophyte in the seed-plants had become, in process of time, retained. The fact that the steps in this process were almost traceable and that the results of retention had been, in the case of the spermophytes, one of the most striking new departures in the evolution of plants, added much force to the suggestion that something closely analogous had happened lower down in the scale of life.

A great difficulty in the old antithetic theory had been to understand the difference between the Bryophytes and Pteridophytes

—the sporogonium of the Moss, with no roots, never became free, while the sporophyte of the Ferns, after a nursing period, protruded a root and became independent. In the light of Dr. Lang's remarks, we might perhaps regard the two series as coming from two different ancestors, the one rootless before retention occurred, the other having already developed the habit of rooting. The old memory of rooting would again obtrude itself and the condition for the evolution of the complex sporophyte be established.

Dr. Lang had alluded to the reciprocal relation of the sporophyte with the retaining generation. To think of the resulting development of the maternal tissue as a " gall " seemed not unhelpful. The **10.0** seed and many other structures might then be interpreted as galls. If we could understand how gall-structures came to be part of the transmissible heritage of plants, much light would be thrown on seed and carpellary structures, and, lower down in the scale, on those peculiar structures in the Jungermanniaceæ, called *marsupia*, which were quite seed-like in some respects. Unless we had some definite light on fixing transmission of this kind, we should have to wait a long time for experimental data. The effect of galls on vegetative structure was very striking; *Uromyces* on *Euphorbia Cyparissias* modified the whole appearance and life of the plant and inhibited reproduction. He thought that a carefully thought-out series of experimental investigations into the conditions of gall production, might throw some light on the subject of that night's discussion.

Mr. A. G. Tansley said that he did not propose to detain the Society long, for he had nothing of any value to add to the remarks that had already been made on Dr. Lang's striking contribution to morphological theory. As a matter of fact he had no particular claim to speak on the subject at all, for he had made no special study of any of the phenomena involved. The suggestion that he should speak that night presumably arose from the fact that he had recently had occasion to enter that highly speculative field, because his studies on the vascular anatomy of the Ferns had forced him to consider the problem of the morphological nature of the fern-frond, and thus, in its turn, the problem of the origin in descent of the Pteridophytic sporophyte—whether it was really to be regarded historically as an elaborated fruit-body, as he had been brought up to believe, or as a plant-body ultimately derived from an algal thallus. Into this highly obscure region of morphological speculation, with a minimum of facts that were really relevant and could be treated on a sound comparative basis, he had accordingly made an expedition, with the result that he had stumbled about in the very dim light, fumbling after half-seen objects in a feeble kind of way, and he certainly did not escape without bruising his shins.

Upon the obscure mass of phenomena involved in this field Dr. Lang had now turned a light which he thought they all hoped might prove the searchlight of truth rather than the *ignis fatuus* of vain speculation. The hypothesis seemed a very promising one, and in accord with all the main classes of relevant phenomena. Its great merit, as the author had remarked, was that it appeared to be open to the test of experiment, and he did not see any reason why they should not have good hope that persistent and well conceived practical tests would eventually bring them to a sure conclusion as to its validity. Though they might never live to see

a freed fertilised egg-cell develop into a prothallus, and an im-
prisoned spore giving rise to a fern-plant, yet some deviations of
development might be obtained which would furnish evidence in
support or in contradiction of Dr. Lang's hypothesis.

Some of them had perhaps during the last twenty years or so
been over-impressed by the magnificent results obtained through
the application of the phylogenetic method to morphology, in the
light of the immensely increased detailed and accurate knowledge
of structure that had accumulated.   As a result some of them
had perhaps been tempted to overlook those fundamental physio-
logical factors—no doubt, in their ultimate analysis, physical
and chemical factors—under which an organism actually develops
in its ontogeny, and   which   no   doubt   played   an   essential
part in determining the form and structure of that organism, as
well as the formation of its reproductive cells.   The epoch-making
work of Klebs, on the side of discovering the factors which actually
determined the formation of different kinds of reproductive cells in
the Algæ and Fungi, remained the nearest approach to an under-
standing of that part of the problem.   For the rest we knew next to
nothing of such factors and of their relation to heredity and to
adaptation.   His own conception, not by any means an original
one, was that while the development of the lower Thallophyta was
very largely controlled by external conditions, working of course
upon, and necessarily modified by, the specific material furnished
by the protoplasm of the species, in other words on the "specific
cell," the higher they went in the plant series, the more the mor-
phogenetic stimuli became internal, so that each stage in the
ontogeny came to be determined by the preceding stage rather
than by external conditions.   With that general conception he
imagined Dr. Lang would agree.   Then came what seemed to him
the fundamental point raised by the new hypothesis.   When the
higher plant, in which a regular alternation of generations was
established, returned to the unicellular condition, to the condition
of the spore or of the zygote, how far did it become emancipated,
so to speak, from this series of ontogenetic stimuli?   In other
words how far did it become capable of responding in a fundamental
way, like its remote ancestors the unicellular Algæ, to environ-
mental influences?   This seemed to him the essence of the
problem which the future had to solve.

Dr. Lang, in replying, said that he had listened with great
interest to the various views that had been put forward that night.
There would be very great difficulty in making an adequate reply
because the remarks that had been made were made from the
phylogenetic standpoint of the old antithetic and homologous
theories of alternation, rather than from the ontogenetic stand-
point which he had adopted.   He himself had experienced
10.15 difficulty in "thinking ontogenetically," if he might so express
it, on this topic. He was somewhat disappointed that almost
every speaker in discussing the paper had departed at once from the
ontogenetic standpoint.   He felt sure that the two ways of looking
at the phenomena ought to be kept apart if progress were to be
made.

[The Meeting was then adjourned.]

THE

NEW PHYTOLOGIST.

THE MORPHOLOGY AND ANATOMY OF *UTRICULARIA BRACHIATA*, OLIVER.

BY R. H. COMPTON

(Gonville and Caius College, Cambridge).

[TEXT-FIGS. 6—12].

*U*TRICULARIA BRACHIATA* was discovered by Sir J. D. Hooker in the Himalayas, and was briefly described by Professor D. Oliver[1] in 1859, the diagnosis being as follows :—

Scapo nudo gracillimo erecto v. descendente 2—4 unc. sæpius 1-floro rarissime 2-floro, foliis reniformibus gracili-petiolatis, corollæ labio inferiore quinquelobato, lobis lateralibus superioribus divergentibus linearibus obtusis, lobo inferiore centrale valde latiore subquadrato rotundatove plus minus abrupte obtuso.

The material used in the present account was collected by Mr. I. H. Burkill in the Sikkim Himalaya, where he found plants growing among moss and foliose Jungermannieæ on the trunks of *Abies Webbiana* at an altitude of 11,000 feet.[2] This material was preserved in spirit and sent to Professor Seward, who handed it to me for examination.

Utricularia brachiata (Fig. 6) is a very small and inconspicuous species. A vertical flowering axis rises above the level of the mosses to the height of two or three inches and bears one or two flowers. A few reniform leaves of very delicate texture also rise into the air. Ramifying among the wet moss are the slender runners which bear tiny bladder-traps and minute tubers.

[1] Journ. Linn. Soc. Bot. iii., p. 187.
[2] Kew Bulletin, 1907, p. 94.

The Runners.

The creeping vegetative axes are fine thread-like structures, circular in transverse section, branching infrequently and irregularly. At certain points four or five branches arise together (Fig. 7 C), one or more becoming an aerial leaf. The mode of branching suggests that the runner is sympodial, but in the absence of true leaves (see below) this could not be settled. At other points short lateral axes are produced, these usually terminating in bladders. The thickness of the axis is fairly uniform, but the bladder-stalks are somewhat narrower.
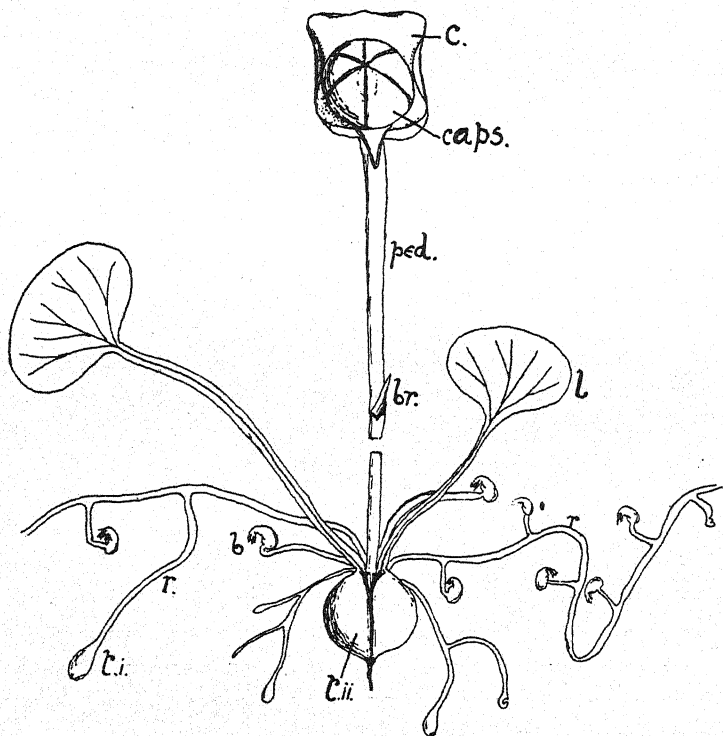
Fig. 6. A well-grown plant arising from a propagating tuber (*t.*ii.); consisting of a tall peduncle (*ped.*) bearing a bract (*br.*) and terminating in a capsule (*caps.*) surrounded by the two segments of the persistent calyx (*c*) From the tuber also arise two leaves (*l*), and a number of runners (*r*) which bear laterally bladders (*b*) and young tubers (*t.i.*) × about 4.

The vascular system of the axis is very simple : a single continuous vessel extends along the axis, enlarging and forking at the nodes. The vessel is largely annular, but here and there spiral

thickenings occur. Transverse walls appear to be entirely absent.
Occasionally the vessel bifurcates without relation to branching of
the axis, the two branches uniting again further along. Surrounding
the vessel is a small quantity of narrow phloem elements, considerably
elongated, and containing a granular substance. The cortex consists
of two or three layers of rather large longitudinally elongated cells.
Small spherical gland-like papillæ appear frequently on the epidermis
of the axes, as outgrowths from small cubical cells (Fig. 7 A, *r*).
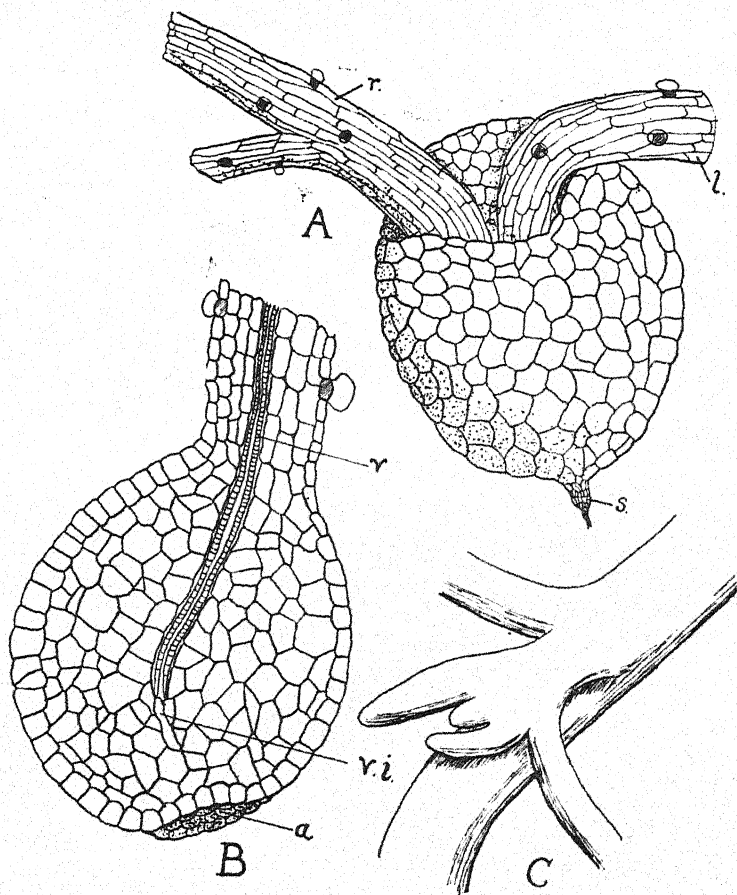
Fig. 7. A.—Tuber shortly after germination, having produced a leaf (*l*)
and a branching runner (*r*); *s*, the remains of the runner which bore the
tuber. B.—Longitudinal section of young tuber still attached to the runner.
v, vascular strand. *v.i.*, cells that will become vascular when the tuber
germinates. *a*, the "eye" or point of germination. C.—Node on a runner,
shewing young shoots arising. × 110.

The Tubers.

At the tip of a runner a swelling is frequently formed, and a small spherical tuber is produced (Fig. 6 *t*.i.) When fully formed the tuber is about 0·5 mm. in diameter, and is opaque owing to the large quantity of storage material contained in its parenchymatous cells.   The storage material is in the form of spherical grains of variable size, translucent in appearance, with a central nucleus, but gave a deep brown colouration with iodine ; some grains after a long time became tinged with violet, and there is little doubt that they consist of one of the starches, perhaps modified by long preservation in spirit.   The stalk thickens its cell-walls close to the tuber on maturity, and the latter becomes detached (Fig. 7 A and B).

The tuber—perhaps the smallest such structure possessed by any Phanerogam—acts as a means of vegetative propagation.   At the distal end from the stalk is found a shallow depression in which new branches and leaves arise exogenously.   The vascular tissue of these new structures becomes continuous with that present *ab initio* in the tuber.

The germinating tuber produces from the concave depression a number of shoots.   Young stages shew a single aerial leaf and a creeping branching axis bearing bladders (Fig. 7, A).   Later the tuber increases greatly in size, reaching 3 mm. broad × 2 high, and new branches are produced ; so that when mature there are present an erect peduncle bearing a single flower and a small lanceolate bracteole, usually two aerial leaves, and a series of ramifying creeping axes bearing bladders and new tubers (Fig. 6, *t*.ii.)

At first opaque, on germination the tuber loses most of its storage material and becomes in consequence translucent in appearance.   This condition persists after germination, and apparently the enlarged tuber comes to act as a water-storage body. The existence of such organs has long been known in *U. montana*,[1] where swellings are produced irregularly on the creeping axis : in the case of *U. brachiata* the water-storing function is a secondary application of the primarily reproductive starch tubers.

The secondary distension of the tuber when it takes up the function of water-storage appears to be due to the mechanical stretching of the cell-walls.   A similar phenomenon has been described in the water-tissue of the leaves of *Rhizophora*,

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[1] C. Darwin.   Insectivorous Plants, 1893, p. 349.
   Hovelacque.   Recherches dans l'Appareil Vegetale, 1888, p. 675.

Geuneraceæ, &c. which may double their thickness in the course of life.[1]

THE BLADDERS.

The bladders (Fig. 8) are numerous; they are elliptical in profile, the length of the major axis being 1·1 mm., and of the
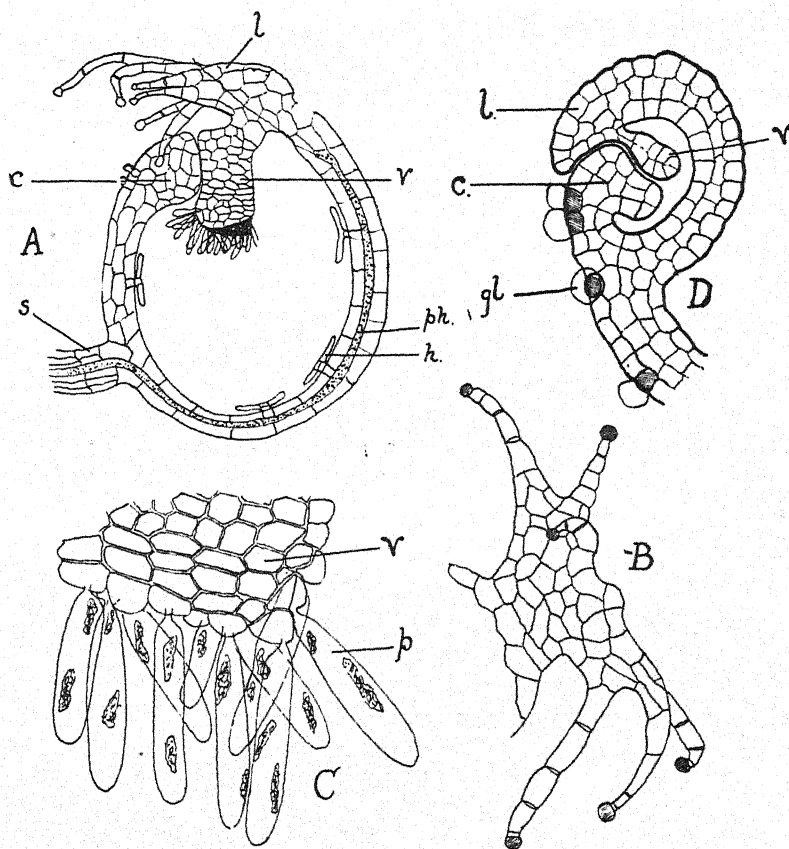
Fig. 8. A.—Sagittal section of a bladder. *l*, upper lip. *v*, valve. *c*, collar. *s*, stalk. *ph*., vascular tissue (phloem). *h*, quadrifid absorptive hair. B.—Upper lip of bladder, fringed with gland-tipped tentacles. C.—Edge of valve (*v*) bearing unicellular processes (*p*). D.—Longitudinal section of young bladder. *l*, upper lip., *v*, valve. *c*, collar. *gl.*, papillate gland. A., × 66. B, C, D, × about 200.

minor 0·75 mm.; laterally they are somewhat compressed. The stalk is attached to the ventral surface, and the vascular tissue (phloem only) after entering the wall of the bladder passes down-

[1] Haberlandt. Physiologische Pflanzenanatomie, 1904, p. 358.

wards and round the base in the median plane, dying out a little above the middle of the dorsal surface. The main body of the bladder is composed of rather large parenchymatous cells, forming a wall about three cells thick; the middle layer is somewhat disorganised. At the collar (peristome of Cohn) the wall is more massive, and furnishes a thick support for the valve.

The valve (Fig. 8, C) is a membrane two cells thick, convex outwards, the cell-walls being much thicker than those of the rest of the bladder. The cells are chiefly hexagonal in outline, and their thickness is very small. The long bristles present in *U. neglecta*, &c., are absent in *U. brachiata.* From the edge of the valve a large number of unicellular processes project inwards.

Lining the inside of the bladder are a number of quadrifid processes of the usual type, with all four arms equal (Fig. 10, F). Gland-like papillæ, similar to those on the axes and leaves, are present on the bladder in great numbers, particularly in the region of the collar: they are abundant on the under surface of the upper lip, and one terminates each of the tentacle-like projections.

The upper lip (Fig. 8, B) is a broad flat structure composed of large parenchymatous cells. It bears in two groups six or eight uniseriate tentacles, each tipped with the spherical gland mentioned above.

Air was present in many of the bladders. Small animals had been entrapped, and in many cases were partially decomposed: the chief prey seemed to be an Entomostracan.

The development of the bladder appears to be similar to that in other species, as described by Goebel[1] and others (Fig. 8, D).

The stalk upon which the bladder is borne resembles the creeping axes, but does not contain a xylem vessel: phloem, however, is present, arising from that of the main axis, and passing into the bladder.

Bladders appear not to be present on the leaves, a feature shared by *U. orbiculata* among the tropical Asiatic species. The peculiar characters of the hairs or antennæ on the upper lip constitute another point of contact with that species.

THE PEDUNCLE.

The peduncle (Fig. 6, *ped.*) arises from the middle of the depression or "eye" in the reproductive tuber, and grows vertically

[1] Ann. Jard. Buit. IX., 1891, Figs. 120, 121 *(U. Warburghi).*

upwards for about 5 cm., the flower being thus carried high above the surface of the moss. About half-way up it bears a small bracteole, lanceolate with a clasping base and a small downward projection. Terminally is borne the single zygomorphic flower, the calyx of which persists round the globular capsule. The diameter of the peduncle is about ·35 mm. and its structure is very simple (Fig. 9). There is a fairly regular epidermis, surrounding a cortical
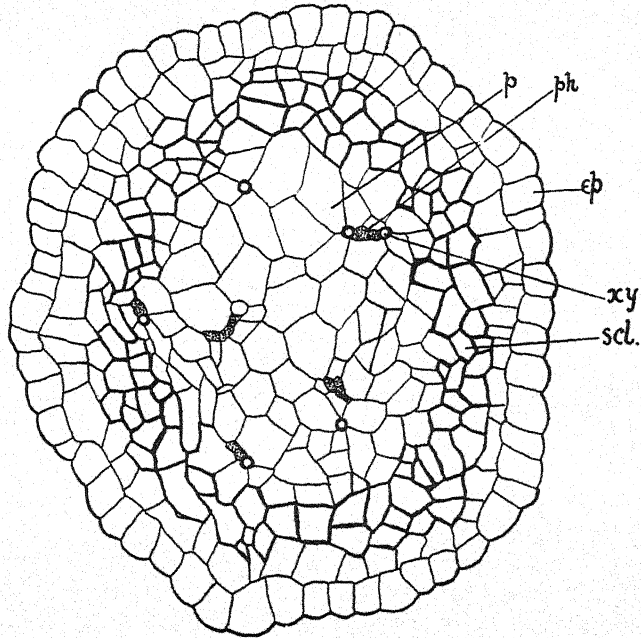
Fig. 9. T.S. of peduncle. *xy*, annular vessel; *ph*, phloem; *p*, pith; *scl*, zone of stereom; *ep*, epidermis.
[The material was somewhat shrivelled].

zone of longitudinally elongated and rather thick-walled cells with oblique transverse walls, but scarcely to be called fibres: inside this is a large-celled pith of elongated parenchyma. Scattered in the pith, but chiefly near its periphery, are small groups of vascular tissue. Altogether about eight annular vessels of small diameter are present, the annuli being widely separated. The phloem is somewhat difficult to make out, but appears to be present in rather greater bulk than the xylem. Sieve-plates could not be found either in the peduncle or in the other vascular structures, and the phloem appears to be largely of the nature of "leitparenchym." While groups of phloem appear to be associated with the vessels, the

orientation of the vascular tissue is irregular. An endodermis could not be discerned.

THE LEAVES.

The aerial leaves are few in number, and though broad, are of delicate texture. They exhibit much variety in size and form: in a few cases the petiole shews a tendency to flatten out (Fig. 10, A). The petiole is cylindrical, and is 1—2 cm. long, broadening distally
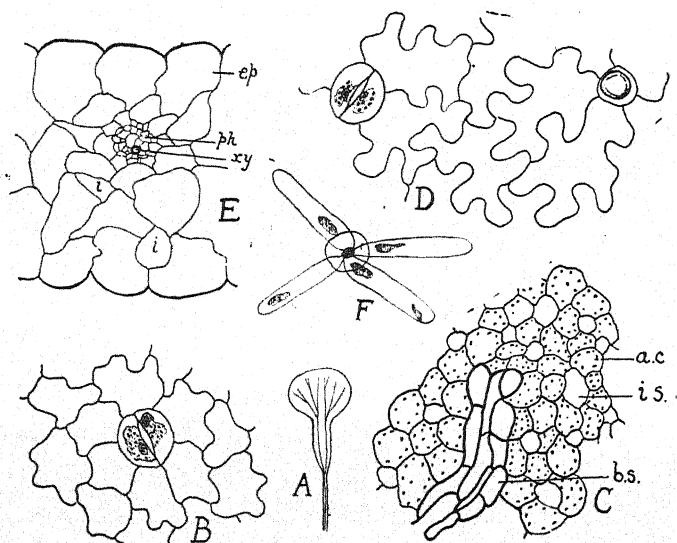
Fig. 10. A.—Leaf showing flattening of the petiole, × 2. B.—Upper epidermis of small leaf. C.—One-layered mesophyll. *a.c.*, assimilating cell. *i.s.*, intercellular space. *b.s.*, blind ending of the vascular bundle, the elongated conducting (slightly thickened) parenchyma being the last to disappear. D.—Lower epidermis. E.—Transverse section of large leaf showing a mesophyll of more than one layer. *ep*, epidermis. E.—Transverse section of large leaf shewing a mesophyll of more than one layer. *ep*, epidermis. *xy*, vessel. *ph*, phloem. *i*, intercellular space. F.—Quadrifid hair from bladder. B, C, D, E, F, × 290.

into an oblate orbicular lamina. The structure of the petiole is almost identical with that of the creeping runners. There is the same axial annular vessel, surrounded by phloem, the cortex is a little thicker, owing, perhaps, to the greater strength required: similar capitate gland-like structures are found both on petiole and lamina. In the lamina the vascular bundle forks repeatedly; the vessels stop short and the ultimate ramifications end blindly in the mesophyll, the vascular tissue there consisting of elongated living parenchyma, apparently of the nature of a bundle-sheath. The lamina consists in its simplest form of three layers of cells—an

upper and a lower epidermis, the cells of the former being smaller and having less interdigitating processes than those of the latter; stomata are present in both, and a mesophyll of one layer, containing many intercellular spaces which communicate with the stomata. In larger leaves and near the base of the lamina in the smaller ones, two or more layers of mesophyll are present. Chloroplasts are present in the cells of the mesophyll and in the guard-cells of the stomata.

THE SEED.

The seeds (Fig. 11) are minute oval bodies about ·4 mm. long, excluding the elongated unicellular hairs, or outgrowths of the cells
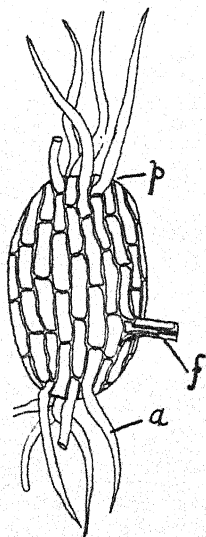
Fig. 11.   Fig. 12.

Fig. 11. Seed. *f*, funicle. *p*, plumular end. *a*, unicellular testal outgrowths. × 79.
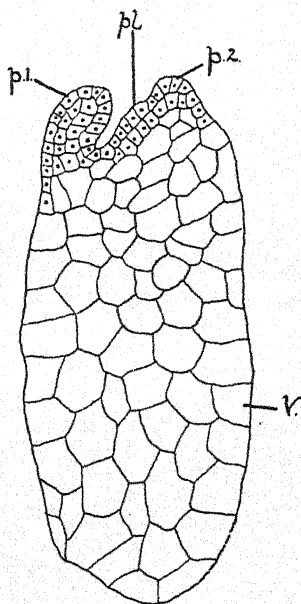
Fig. 12. Longitudinal section of embryo, in plane at right angles to the funicle. *v*, mass of storage cells, not meristematic. *pl*, plumule. *p*.i., *p*.ii., first and second papillate protuberances. × 190.

of the testa, which arise at both ends. This character sharply separates *U. brachiata* from its near ally, *U. orbiculata*, in which the testal outgrowths are short, all directed to one end, and glochidiate. The testa consists of a single layer of longitudinally elongated, rather thick-walled cells: no micropyle being discernible in the ripe seed. The funicle is attached laterally, nearer the end of the seed

opposite to the plumule. In the region of the funicle is present a small quantity of extra-embryonal food tissue, whether endosperm or perisperm being of course unascertainable: this is completely resorbed over the greater part of the embryo. This fact appears to be exceptional in an order characteristically devoid of "endosperm."

The embryo (Fig. 12) is a mass of tissue about ·36 mm. long, shewing distinct polarity. Differentiation is but slight. The whole posterior mass of cells is a passive reserve store-house, and only the anterior end of the embryo is meristematic. Cotyledons (in the ordinary sense of the word) are absent, and two papillæ of unequal size are the only protuberances. The "plumule" lies between, and may be regarded as arising laterally on one papilla, or preferably as producing the smaller papilla at a period subsequent to the larger. The whole structure is in some degree parallel to that in U. orbiculata.[1]

The seeds are borne in a globose capsule, on a spongy free central placenta. From their small size and hairy appendages, as well as from the habitat of the plant, they appear to be adapted for dispersal by wind.

GENERAL CONSIDERATIONS.

The question of the morphological value of the various vegetative structures found in the genus Utricularia has given rise to much discussion from various points of view. Hovelacque[2] considered that the runners are "feuilles reduites à leurs nervures." A similar view was taken by Pringsheim[3] and others in such cases as U. vulgaris, owing to the definite growth of the apparently lateral branching bladder-bearing structures in that species. This view has been developed by Goebel, who succinctly states the arguments in his "Organography."[4] Schenck[5] took the opposed view that the runners are caulome structures and are to be compared with the stolons of the strawberry. Schimper[6] took a similar view, with the addition of the theory that the leaf-like organs of many species of Utricularia have arisen by a flattening of caulome structures.

The simple view, viz., that the "leaves" are phyllomes and the runners caulomes has also been held, but there now seems to be no

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[1] Goebel. Ann. Jard. Buit. IX., p. 59 and Pl. X.
[2] Comptes Rendus CV., 1887, p. 692, CVI., p. 310.
[3] Monatsber. d. Königl. Akad. d. Wiss., Berlin, 1869.
[4] Engl. edition, 1905, II., p. 239.
[5] Pringsh. Jahrb. XXIII., 1886, p. 218.
[6] Bot. Zeit., 1882, p. 241.
    Bot. Centralb. XVII., p. 257.

doubt that this view is untenable, owing to the innumerable transitions which are found between runners and "leaves," and the fact that bladders are found indifferently on both forms of organ. The conclusion is irresistible that both runners and "leaves" belong to the same morphological category. The alternative views we have to consider are briefly :—

1. The "leaves" are of the nature of phyllomes and the creeping runners are specialised leaves.

2. The runners are caulome structures, and the "leaves" have been derived from similar organs by a process of flattening.

The arguments for the former view, stated by Goebel, depend primarily on a supposed analogy between the bladders of *Utricularia* and the remarkable tubes or utricles of the closely allied genus *Genlisea*. As Goebel remarks, there can be no doubt that the tubes of *Genlisea* are modified leaves.

These tubes are curious forked structures with a highly developed eel-trap arrangement for catching small animals. The structure of these utricles, as Charles Darwin called them, has been thoroughly investigated,[1] and there is no need to enter into it here in detail. These eel-trap structures have been generally assumed to be homologous with the bladders of *Utricularia*. It appears, however, that they may well be of quite distinct origin and nature. It is very difficult to imagine the mode in which the transition from one form of trap to the other could have been effected. Both bladder and utricle are well-defined and highly specialised organs, and the range of variation in the two genera in the essential features of each form of apparatus is relatively small: variations in form of the upper lip of the *Utricularia*-bladder are abundant, and the details of arrangement of the trichome structures shew some diversity in the different species; but there exists (so far as is known) nothing, normal or pathological, which points to any direct transition from such bladders the utricle of *Genlisea*, or vice versâ, or to the derivation of both bladder and utricle from an intermediate ancestral form. Another fact which supports this position is that the utricle of *Genlisea* is, as regards the leaf from which it was derived, a terminal structure; whereas the *Utricularia*-bladder is borne laterally. Though this is

[1] F. Darwin in C. Darwin's "Insectivorous Plants," 2nd Revised Edition, 1893, p. 360, et seq.

Goebel. "Pflanzenbiologische Schilderungen," II. (1893), p. 121.
    ,,   Flora LXXVII., 1893, p. 208.

Warming. Vidensk. Meddel. Nat. For. Kjøbenh., 1874, 33, t. 5, 6.
    ,,   Ann. Sc. Nat., ser. 2, XI., p. 165, t. 5.

a small point it contributes to the support of the view that bladder and utricle should not be homologised.

A more important argument, which, however, appears to have been overlooked in previous discussions, is derived from the existence of a South American species of *Genlisea*, *G. filiformis*. This plant was described by A. St. Hilaire[1] in 1833, and later authors have to a large extent copied the description with its imperfections. Darwin,[2] however, recorded the fact that *G. filiformis* does not bear the typical utricles found in the other species, but on the other hand bears on its rhizomes a number of typical Utricularian bladders: these he considered to shew signs of reduction on account of their small size and the fewness of their absorptive hairs. Darwin asks: " What are we to infer from these facts ? " It appears clear that a just inference is that the typical utricles of *Genlisea* are not homologous with the bladders of *G. filiformis* and of the species of *Utricularia*.

As it thus appears that the argument from the leaf-nature of the *Genlisea* utricle is untrustworthy, even if not untenable, let us examine the actual facts in regard to *Utricularia* itself more on their merits.

There can be no doubt that the small bracts on the peduncle of *Utricularia* are true phyllome structures. It seems to be a general principle that the peduncle is, relatively to the rest of a plant, primitive in structure: and since the bracts of the *Utricularia* peduncle agree so closely with similar structures in more " normal " plants, the conclusion that they are of phyllome nature is irresistible. Now Schimper[3] described leaf-like organs arising in the axils of the peduncular bracts of *U. cornuta*. He remarks, " Wahrscheinlich ist es mir daher, dass die sogenannten Blätter Kaulomnatur besitzen." The biological significance of this fact is clearly that leaf-like structures are only formed in air, and that a runner of the *Utricularia* type would be quite useless in such a position.

In some species (e.g., *U. orbiculata*) the embryo bears two papillæ, which are sometimes homologised with cotyledons : these may grow out into runners, and hence it is concluded that the runners are derived from cotyledons and therefore from foliage leaves. But it must be remembered that the homology of cotyledon and foliage-leaf is still a matter of dispute : and what is more

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[1] Voyage au District des Diamans, II., p. 428.
[2] Insectivorous Plants, p. 364.
[3] Bot. Zeit., 1882, p. 243.

important, there is little reason for relating the papillæ to cotyledons: in some aquatic species a large number of such papillæ are present, and in *U. brachiata* the two papillæ arise successively and not simultaneously on the embryo.

Goebel remarks, " We find all transitions between foliage-leaves and stolons," but the nature of these transitions rather points to the reverse view to that which he upholds. The flattened " foliage-leaves " may branch repeatedly, and the branches may become runners or leaves[1]: their veins may be prolonged into runners beyond the lamina.[2] Also some leaves are found shewing conditions which suggest a progressive flattening rather than reduction (Fig. 5, A).

The further fact that " leaves and stolons are alike in their position on the seedling,"[3] clearly does not support one theory rather than the other.

Numerous other facts point to the view that the leaf-like organs are of caulome nature. The runners are of unlimited growth, a feature unknown among true leaves.[4] It is true that a possible parallel may here be drawn with the fronds of certain Ferns, but it must be borne in mind that it is by no means certain that the fern-frond is homologous with the angiosperm leaf; and moreover that a parallel between groups so far removed in the natural system of classification can have little value. Further, the transformed leaves of such water-plants as *Limnophila heterophylla*, and *Ranunculus aquatilis* are structures of limited growth, and very unlike the runners of the land species of *Utricularia*.

Then again the runners may at certain points produce rosettes of leaves and new runners, in a manner strongly suggestive of the stolons of such a plant as *Ajuga reptans*, in which the stolon bears at a node an erect flowering axis and a number of diageotropic lateral shoots. Similar phenomena in leaves are very rare, being confined to Ferns (with respect to which the same objections apply), *Begonia*, *Bryophyllum* and one or two other cases.

The formation of tubers of various types is frequent in the genus *Utricularia* : they are always developed by a swelling of the runners, either terminally or at a point in the course of the runner.

[1] Goebel. Ann. Jard. Buit. IX., 1891, Plate VI., &c.

[2] Ridley. Ann. Bot. II. On a new species of *Utricularia*, &c., p. 305.

[3] Goebel. Organograpny, Engl. Ed. II., p. 240.

[4] Such a case as *Tumboa* has clearly no real significance here as a parallel.

Now tubers are quite unknown upon true leaves, while of frequent occurrence on stolons. There is thus a strong presumption that *Utricularia* will also exemplify what appears to be a universal principle.

The view here advocated, that the runners of *Utricularia* are caulome structures and that the " leaves " are of the nature of phylloclades, has the merit of bringing a very anomalous genus into line with the majority of flowering plants. It requires no such remote morphological assumptions as the opposed view involves: and is without the theoretical demerit of the contrary view, in that it does not tend towards an abolition of morphological categories.

ON TWO NEW MEMBERS OF THE *VOLVOCACEÆ*,

BY B. MILLARD GRIFFITHS, B.SC.

(*University Scholar, Birmingham*).

[[TEXT-FIGS. 13—15.]

SINCE October, 1908, I have been carrying on an investigation of the Algæ of Stanklin Pool, near Kidderminster, largely with the view of accumulating data concerning any possible winter stages of these plants, and also to ascertain to what extent they pass the winter in the vegetative condition.

This work, which is still proceeding, was undertaken at the suggestion of Dr. G. S. West, and is being carried out under his direction.

The pool is a very old one, fed by bottom springs, and has yielded a number of interesting algæ, among which two species of the *Volvocaceæ* have been particularly noticeable. As these are both forms of considerable interest, it has been thought best to issue a separate article on them.
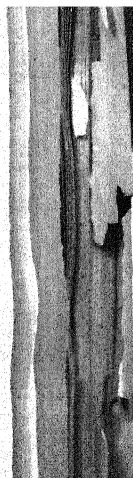
Pyramimonas delicatulus, sp. n.

A small motile organism, which has been found to belong to the *Polyblepharideæ*, occurred in abundance in the autumn of 1908. It belongs to the genus *Pyramimonas*, Schmarda (1850),[1] and is the first member of the sub-family *Polyblepharideæ* to be recorded for the British Isles.

Collections of algæ from various parts of the pool have been made every alternate week since October 17th, 1908. *Pyramimonas* was first noticed on November 14th, 1908. It occurred sparingly among *Elodea* and various species of *Potamogeton*, but abundantly in the soft mud of the shallower parts of the pool. The temperature of the water at this date was 8·5°C.[2] The alga became more plentiful up to December 12th, when the temperature had steadily and uniformly gone down to 3·4°C. At the end of December, the temperature suddenly sank to 1·3°C and the alga became less abundant. The low temperature was maintained during the beginning of January, 1909, and by the middle of the month the alga had almost entirely disappeared. At the beginning of February, 1909, the temperature rose to 6·5°C., and the organism became more plentiful again. No specimen was found in any instance in collections obtained from the surface water.

Pyramimonas delicatulus moves at considerable speed through the water. It appears to swing from side to side as it moves, its motion resembling rather the Flagellate than the Chlamydomonad type. Its four cilia are strong and thick. They do not taper, but appear to end abruptly, and can easily be seen without any staining. When the organism is at rest the cilia lie back over the body of the cell. When under observation the alga very often comes to rest with its ciliated end downwards, and never the other way.[3] This position may be assumed owing to the attempts of the organism to travel towards the bright light. It is stopped by the glass slide and comes to rest in the position observed.

The chloroplast is cup-shaped, with the sides deeply cleft into four lobes, each of which has a small incision at the extremity. The incision is not visible except in the anterior axial view (Fig.

[1] Consult Dill. Jahrbücher für wiss. Botanik, Heft. 3, Band XXVIII., 1895, pp. 351-353; also Blochmann, Die Mikroskopische Thierwelt des Süsswassers, Abt. I., Protozoa, 1895. p. 62.

[2] All temperatures were surface temperatures taken at a depth of 4 to 6 inches.

[3] Consult Dill, *loc. cit.*, plate figure 46. This shows *P. tetrarhyncus* in the exact position that *P. delicatulus* assumes.

13, E), or when the organism is distorted with re-agents so that the lobes are more or less divaricated (Fig. 15, A).

There is a large pyrenoid in the chloroplast, situated in the thick posterior portion, behind the fusion of the lobes. It is surrounded by a starch sheath (Fig 13, A, B, C). Behind the pyrenoid in the line of the cell axis is a small flask-shaped cavity, which
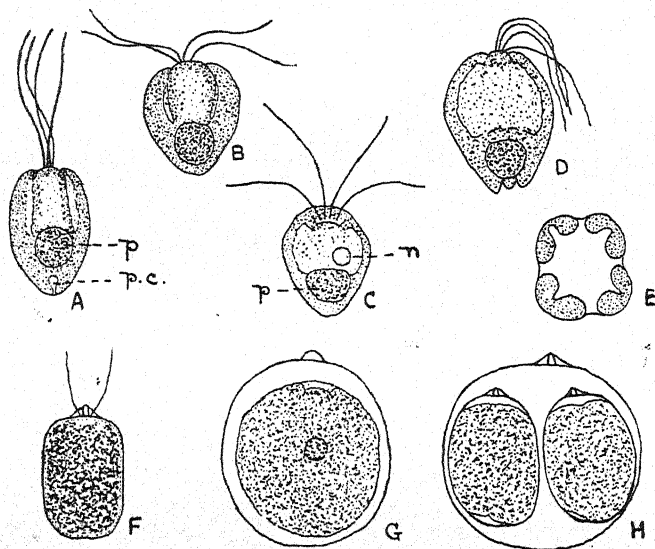
Fig. 13. A-E., *Pyramimonas delicatulus,*sp.n. A, Vegetative form; B, Larger form showing lobation of the cell : C., Form showing anterior depression with cilia arising; D, Form with lobed extremity of chloroplast; E, Anterior axial view, showing extremities of lobes of chloroplast with incisions (cilia not shown). F-H, *Chlamydomonas* sp. F, Vegetative stage; G, Large mother-cell; H, Mother cell with two daughter-cells formed by longitudinal division. *n*, nucleus; *p*, pyrenoid; *p.c.*, posterior cavity in chloroplast (×800.)

opens out at the posterior extremity of the chloroplast (Fig. 13, A, Fig. 14, A). In some specimens the latter is divided into four blunt lobes, but this is not usual (Fig. 13, D).

I was unable to find a pigment spot in any of the many specimens examined. Neither was I able to find vacuoles at the base of the cilia. The search for the latter is made very difficult on account of the cup-shaped depression at the anterior end of the cell, in which the cilia originate, and the organism cannot be made to take up a position favourable for observation.

Division. Vegetative multiplication takes place by means of longitudinal fission. This was commonly observed in all the collections examined. The ordinary vegetative cell is at first elongated (Fig. 14, A). It soon becomes broad and heart-shaped

(Fig. 14, B), the pyrenoid increasing simultaneously with the growth of the cell.   The pyrenoid shows signs of elongation transverse to the cell-axis (Fig. 14, A) and eventually it divides into two equal portions (Fig. 2 B).   At the same time the chloroplast begins to split, starting at the posterior end, the line of division running
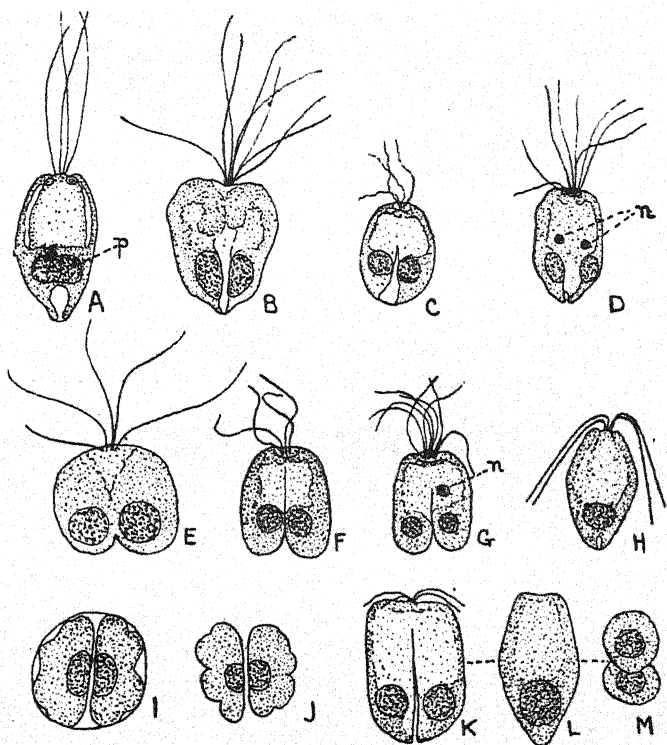
Fig. 14. *Pyramimonas delicatulus.*   A, Pyrenoid elongating;   B, Pyrenoid divided;   C, Chloroplast dividing;   D, Nucleus divided;   E, Form with five cilia;   F, Cell-membrane invaginating;   G, Form with eight cilia;   H, One of the two individuals produced on the completion of fission;   I-J, Posterior axial view;   K-M, Dividing individual (× 800).

through the small flask-shaped cavity.   The cell-membrane,[1] up to this stage, has not shown any sign of division; it is merely the chloroplast that is dividing.   The line of division passes through the thick posterior portion of the chloroplast, between the halves of

[1] Like other members of the *Polyblepharideæ*, *Pyramimonas* does not possess a cell-wall of secreted cellulose.   The protoplasm of the cell in contact with the surrounding water, is of a firmer consistency than the inner portion.   The outer differentiated layer is protoplasmic and therefore differs essentially from the secreted cell-wall of *Chlamydomonas*.   In this sense, therefore, *Pyramimonas* cannot be said to possess a cell-wall. Hence " cell-membrane " is used in preference to the less correct term.

the pyrenoid, dividing it into two parts, each part having two complete lobes of the original chloroplast (Fig. 14, B, C. I, J).

The incisions at the extremities of the lobes play an important part, for by their increasing depth, the four lobes of the new chloroplast are formed.

Before this takes place however, the original cell-membrane becomes invaginated posteriorly in the median line (Fig. 14, E). The invagination gradually deepens and passes between the two halves of the chloroplast (Fig. 14, F, G, K), so that the cell becomes divided into two lobes, joined together at the ciliated end.

The cilia increase in number from four to eight. The new cilia do not always appear at the same time. Specimens were noted with five (Fig. 14, E), six and seven full-grown cilia. The appearance of the cilia seems irrespective of the state of the division of the cell, but no case was observed in which they arose before the division of the pyrenoid.

The nucleus usually lies in the cup of the chloroplast, about half-way up, on the side of one of the lobes (Fig. 13, C, Fig. 14, G). It is often difficult to observe in the division stage, but it was fully made out in two cases. It divides into two, and these take up positions as seen in Fig. 14, D.

The fission of the cell is continued until two separate and rather elongated organisms are found. These proceed to repeat the same cycle of growth and division.

No amœboid alterations in the shape of cell were observed[1]; the only change noticed was the greater stoutness of the cell as the period of fission approached.

No encysted state was observed.

Pyramimonas delicatulus is exceedingly susceptible to adverse conditions. Attempts to make cultures either in the original water or with Knop's solution were unsuccessful. If the temperature rose above 9°C, the organisms were killed and partially disintegrated. Keeping in wide glass tubes for more than a few days was equally fatal, even at a temperature of 6 or 7°C.

Effects of Formalin. Weak solutions of formalin are so widely used for fixing and preserving algæ that some remarks upon the effects produced on *Pyramimonas* may be of value. All attempts at preserving this alga in solutions of 4%, or under, proved disastrous.

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[1] In this respect *Pyramimonas* appears to differ from the other members of the *Polyblepharideæ*. Consult Teodoresco on *Dunaliella*, Beihefte zum Bot. Centralblatt. Band XVIII., Abt. I., Heft. 2, 1905, p. 217.

The cell-membrane becomes swollen out into great blisters (Fig. 15, A, B); the lobes of the chloroplast are widely divaricated (Fig. 15, D, G), and eventually the latter becomes a shapeless green mass (Fig. 15, C, E, H).
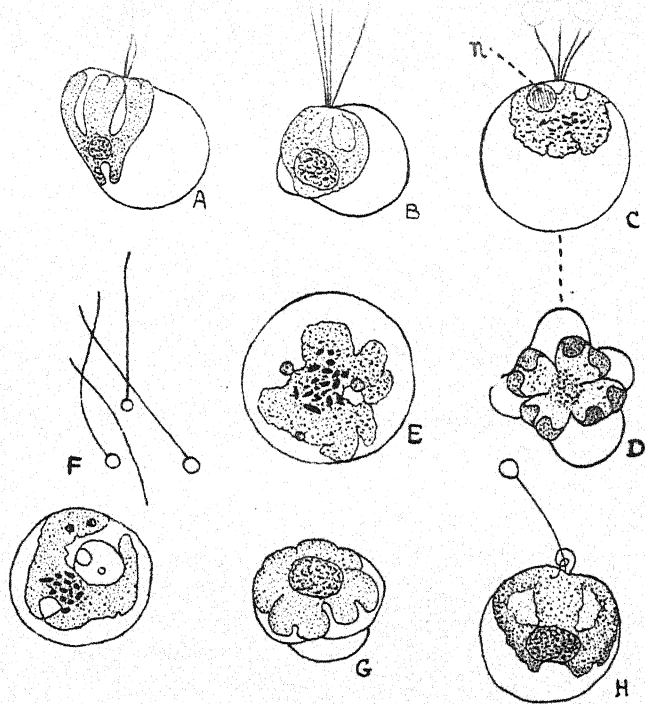
Fig. 15. *Pyramimonas delicatulus.* Drawings to illustrate effects of weak solution of formalin.   A-B, Cells beginning to blister;   C, Completely spherical cell, chloroplast disintegrating, cilia swollen at extremities;   D, Anterior axial view of same cell as C at earlier stage ; E, Posterior axial view, showing scattered starch grains of pyrenoid sheath ; F, Spherical cell, swollen cilia thrown off; G, Oblique posterior axial view, showing lobes of chloroplast ; H, Spherical cell, one cilia swollen, another twisted up (× 800).

The pyrenoid disintegrates and the starch grains surrounding it are scattered (Fig. 15, C, E, F). The cilia swell at the tips (Fig. 15, C), or twist up (Fig. 15, H) and are often thrown off altogether (Fig. 15, F). The cell-membrane finally becomes distended and spherical (Fig. 15, C)[1] and sometimes disintegrates.   The process occupies

[1] Consult Teodoresco *loc. cit.*, p. 219.   *Dunaliella* is affected in a very similar way when the concentration of the saline water, in which it lives, is altered.

a few minutes and during this time the distortions of the cell-membrane make the construction of the chloroplast very obvious.

On the other hand, if strong formalin is used, no such effects are produced. A solution of 20% formaldehyde (made by adding an equal volume of 40% solution to the water in which the organisms are), causes no distortion beyond a very slight shrinkage of the cell. The cilia do not exhibit swelling at the extremities, but merely lose their stiff appearance and become irregularly flexuose. (Fig. 14 D, shows a specimen fixed in this way). Subsequent dilution of the solution to 2 or 1% does not cause osmotic blistering.[1]

Slight shrinkage of the cell is also produced by strong iodine solution. Most of the specimens in Figs. 13 and 14 are fixed in the latter

Remarks on the Cilia. On referring to Fig. 15, C, F and H, it will be noted that the cilia show a peculiar swelling at the extremities. It is not a case of curling up, because under such circumstances the unaltered part of the cilium would run to the side of the swollen part, and not to the middle. The cilium does not become very much shorter, as it apparently does in true cases of curling up (compare the two cilia in Fig. 15, H). Several examples of the latter were noted, but these differed totally from the swollen cilia.

In the living state the cilia are thick and firm, but at death they lose their firmness (Fig. 13, D), except when the cell has become over-turgid through osmotic action induced by re-agents. The rigidity of the cilia under the latter conditions is quite remarkable (Fig. 15, B). The absence of blisterings on the sides of the cilium, and the symmetry of the swelling at the extremity, seems to suggest that in this organism, the cilium is not a homogeneous rod but rather a structure in which the peripheral part is of a denser character than the more central portion.

*Diagnosis :—*Pyramimonas delicatulus, sp. n. Cellulæ parvæ, cordatæ vel compressæ, leviter quadri-lobulatæ; lobi chloroplasti cum incisione parva in extremo, cum excavatione pyriforme parva in parte posteriore. Stigmate caret. Long. 20-26μ, lat. 11-16μ.

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[1] Dr. West suggests that the peculiar effect may be due to the presence of formic acid in ordinary commercial formalin. Possibly in the dilute solution the irritating action of the acid is greater than the fixing power of the formaldehyde. In the strong solution, however, the formaldehyde fixes the organism instantly. The acid has no irritant effect on the dead protoplasm and consequently no distortion takes place.

Hab. In mud and among water-weeds, Stanklin Pool, near Kidderminster, Worcestershire (November, 1908—January, 1909).

All the figures are drawn with the aid of the *camera lucida*.

CHLAMYDOMONAS, sp. n. (?).

In collections taken from among *Potamogeton lucens*, a fair number of a species of *Chlamydomonas* was found. Reference to the synopsis of this genus given by Dill,[1] and also by Wille,[2] failed to find any species to which this could be referred. The most prominent characteristic of the organism was a distinct, well-marked channel running up through the transparent "beak" ("hautwatz"). It stood out so plainly that there appeared to be a small peg projecting from the anterior extremity of the cell (Fig. 13, F). The two cilia are not easy to see, even after staining; they arise one on either side of the channel in the beak (Fig. 13, F).

Multiplication was observed in one case. The cell becomes large and rounded. The contents round off and divide longitudinally. The resulting daughter cells become invested with a cell-wall, but are at first of a more rounded form than the older vegetative cells.

The chloroplast is exceedingly granular, and it is difficult to make out pyrenoid or stigma.

[1] Dill. Jahrbücher für wiss. Botanik, Heft. 3, Band XXVIII., 1895.

[2] Wille. Algologische Notizen IX.-XIV., Christiania, 1903.

University of Birmingham   February, 1909.
    Botanical Laboratory.

ON AN ABNORMAL GYNŒCEUM IN *STACHYS SYLVATICA*, LINN.

[Text-Figs. 16, 17.]

A PLANT of *Stachys sylvatica* Linn., was gathered near the village of Medstead in Hampshire, in September, 1903 on account of an abnormal appearance of the flowers and the specimen was placed within the leaves of a book to dry. Circumstances have until recently prevented me from examining the plant more closely.

The specimen consisted of two flowering shoots, which for convenience I shall denote as I. and II. On I. there were borne five verticillasters or false whorls of expanded flowers and seven on II., together with a few verticillasters of small flower-buds towards the apex of either inflorescence. The general characters of the plant, leaves, etc. were quite typical.

The flowers were examined by the method usually employed when dealing with dried plants, *i.e.*, they were boiled one by one in a little water in a test-tube for a few minutes to soften and expand them, after which they could be easily dissected under a magnifier and the form and the relation of the several parts observed. The three outermost whorls of the flowers presented no points of any special interest, but the lower lip of the corolla was rather less expanded and the stamens were relatively shorter than was the case in ordinary flowers from other plants which I examined at the same time for purposes of comparison. The gynœceum, however, was abnormal in every flower of both inflorescences and possessed some characters of exceptional interest.

The form of the pistil in I. is shown in Figs. 16 (A—F) and 17, A, proceeding from the base of the inflorescence, or the lowest false whorl, towards the apex, that of II. in Fig. 17, B—E in the same order. The gynœceum of an ordinary flower is shown in Fig. 17, F for comparison. All the figures are enlarged to four times the natural size of the structures.

In the flowers from the first or lowest verticillaster of I. (Fig. 16, A)which show the smallest amount of modification in the pistil, the ovary is much elongated, so that it is of nearly the same length as the style ; the four ovules which it contained were aborted as might have been expected, and this was found to be also the case in all the flowers examined. The style was much shortened and clothed

with a covering of long hairs, while in normal flowers the whole
pistil is glabrous. This abnormal development of hairs, which was
found in every flower, shows a step towards the phyllody seen in
the pistil in the higher verticillasters.
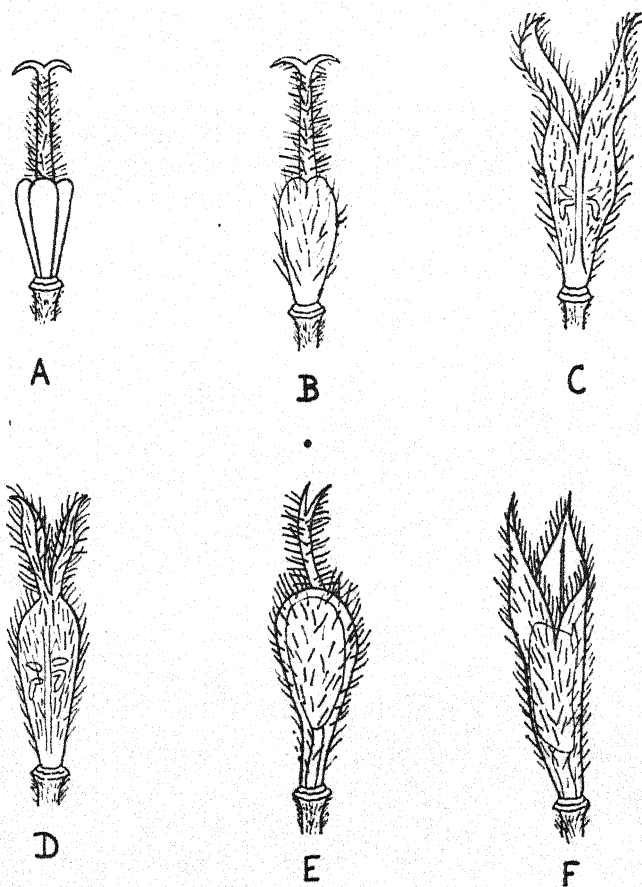
Fig. 16. Abnormal gynœcia of *Stachys sylvatica*. Inflorescence I. A,
from lowest verticillaster; B, from second and third verticillasters; C, D,
from fourth verticillaster; E, F, from fifth (uppermost) verticillaster. See
Text.

In the second and third verticillasters of I. (Fig. 16, B) the ovary
has become still more enlarged and in some cases bears a sparse
covering of hairs, while the style is as before densely hairy.

In the next or highest false whorl but one (Fig. 16, C and D) the
gynœceum has become considerably modified and shows well-
marked phyllody, consisting of two hairy, more or less leaf-like
carpels, united by their edges for more than half their length. In

texture they are membranaceous and the aborted ovules can be discerned through them.

The three flowers of the uppermost verticillaster (Fig. 16, E and F, and 17, A have the gynœceum most modified. One of these (Fig. 16, F) shows pronounced phyllody while in another one E we see a more advanced stage of that drawn in Fig. 16, B in that the ovary has become still more enlarged and the style correspondingly shorter. But the most curious feature in these two (Fig. 16, E and F) was that the floral axis in both flowers had produced a stalked flower-bud, which had grown up inside the ovary and the outline of which was just visible through the carpel wall as I have shown by the thin internal line in the drawings. In one of these flower-buds, that shown in F, the calyx and corolla could be distinctly made out by careful dissection, but only three epipetalous stamens with the typical diverging anthers could be found, and the centre was occupied by two leaf-like carpels quite separate from each other. In the other flower-bud (E) dissection was more difficult as the parts were somewhat distorted, the five calyx-teeth were not plain, there were four separate rudiments of petals and to three of them anthers were adhering; I could find no trace of the fourth stamen. The two carpels were separate and foliaceous, the apex of each was bent outwards representing a rudimentary stigma and each bore two rudimentary ovules.

The gynœceum of the third flower of the uppermost whorl of I. presented the much reduced form shown in Fig. 17, A, *viz.*, a small rounded body, slightly exceeding 1 mm. in diameter carried on a short stalk and bearing at its apex three small erect pieces. The drying and subsequent boiling had obliterated the internal structure and I was unable to ascertain what it represented morphologically.

In inflorescence II. the pistil had undergone much the same modifications as in I. In the two lowest verticillasters of flowers (B) it closely resembled that in the three lowest false whorls of I. In the third and fourth (Fig. 17, C and D) it consisted of two leaf-like carpels united by their edges for rather more than half their length.

In the sixth false whorl (Fig. 19, E) the two carpellary leaves have become quite separate, they are unequal in size and show no trace of ovules, and between them at their base is a minute rudimentary flower-bud.

Of the three flowers constituting the highest verticillaster, two contained each a short stalk, due to the elongation of the internode

between the stamens and pistil, bearing at its apex a very small flower-bud with a rudimentary carpellary leaf on either side of it. The third flower had at the end of a short stalk a group of five similar small rudimentary flower buds, each partly inclosed by a pair of small unequal carpellary leaves; the largest of these buds measured barely 2 mm. in length.
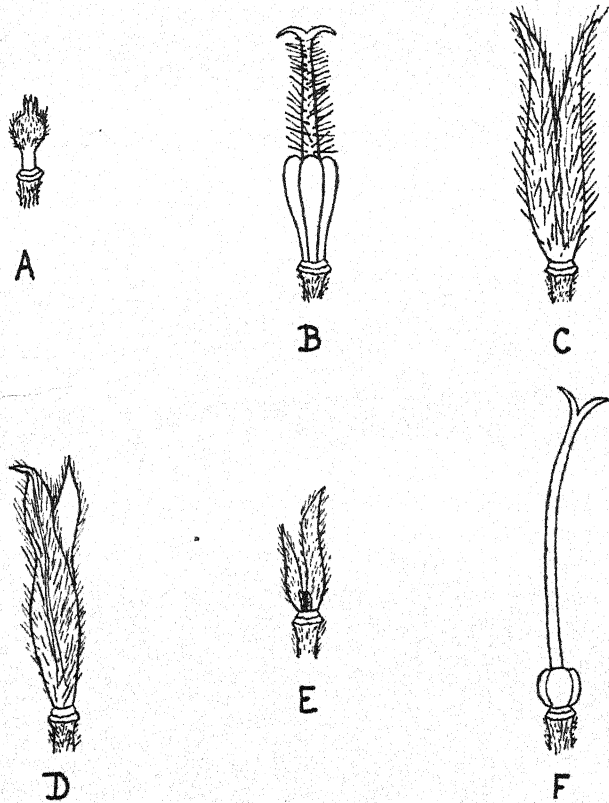
Fig. 17. Abnormal gnyœcia of *Stachys sylvatica*. A, Inflorescence I., reduced gynœceum from a flower of the uppermost verticillaster. Inflorescence II. B, from two lowest verticillasters; C, D, from third and fourth verticillasters, E, from sixth verticillaster; F, normal gynœceum of *Stachys sylvatica*. See Text.

This peculiar abnormality, which was mostly clearly shown in the uppermost false whorl of I, where the axis of the flower produces one or more flower-buds in the centre of the flower is termed by Masters[1] *median floral prolification*. He refers to another very similar example,[2] amongst others, which was found in

[1] M. T. Masters, " Vegetable Teratology," p. 119.

[2] Loc. cit., p. 125.

a plant belonging to a closely related Natural Order, *viz.*, Anchusa ochroleuca belonging to Boraginaceæ, "in which the pistil consisted of two leaves situated antero-posteriorly on a long internode with a small terminal flower-bud between them."

The phyllody of the pistil, in which we find this part of the flower composed of two foliaceous carpels, furnishes additional evidence for what has been already ascertained by tracing the development, *i.e.*, the gynœceum in Labiatæ, as well as in Boraginaceæ, is really bi-carpellary, although the ovary is quadrilocular. This affords an instance in which a teratological phenomenon is able to throw light on the morphological nature of a structure.

The principal facts observed in this specimen may be summed up as follows :—

1. The pistil in every flower had undergone a certain amount of teratological modification, one result of which was the abortion of all the ovules.

2. The modification of the pistil increased in extent acropetally, *i.e.*, in the same order in which the sucessive verticillasters of flowers were developed.

3. The changes were observed to have taken place generally in the following order :—

(*a*) The ovary was much enlarged, especially in length and the style was correspondingly shortened and very hairy.

(*b*) The ovary was represented by two foliaceous hairy carpels usually united by their edges for rather more than half their length.

(*c*) The floral axis produced at its apex one or more flower-buds, the carpels either being of the same structure as before, or becoming to a greater or lesser degree aborted. At the same time there was a tendency for the internode between the stamens and pistil to become elongated.

Botany School,   A. W. BARTLETT.
        Cambridge.

NOTE ON THE SPOROPHYLL OF *LYCOPODIUM*

INUNDATUM.—A CORRECTION.

[TEXT-FIGS. 18, 19.]

I N a recent paper Dr. Lang[1] refers to my figure of the sporophyll
of *Lycopodium inundatum*, published in last year's volume of
this journal.[2] He states that "the sporophyll does not possess the
peltate form shown in Miss Sykes' figure." Dr. Lang has been
most kind in explaining to me his reasons for this statement, and I
feel that some comment on my previous description and figures of
this species is necessary. The text-figure referred to is not taken
from an absolutely median section of the sporophyll, but from one
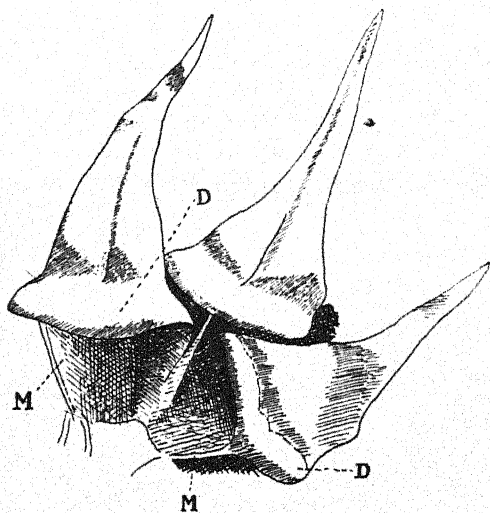
Fig. 18.   Fig. 19.

Fig. 18.   Three sporophylls of *L. inundatum*; showing *D*, the dorsal flap,
and *M*, the descending membrane.
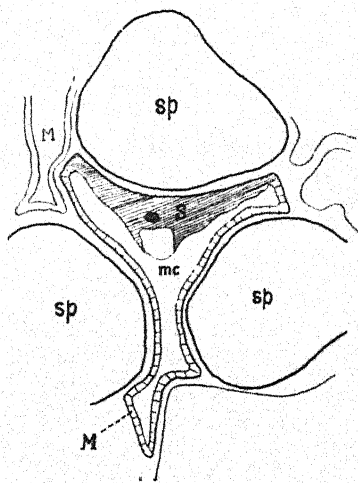
Fig. 19.   Tangential section of a sporophyll stalk (*s*), shewing *M*, the
descending membrane, and *mc*, space formed by mucilaginous degeneration.

slightly to the side of the middle radius. In Fig. 56, Pl. 2, of my
paper (cf. Fig. 18 of this note) I have unfortunately omitted to figure

[1] Lang, W. H.   Preliminary Statement on the Morphology of
the Cone of *Lycopodium cernuum* and its bearing on the
affinities of *Spencerites*. Proc. Roy. Soc., Edin., Vol. XXVIII.,
1908.

[2] Sykes, M. G.   Notes on the Morphology of the Sporangium-
bearing organs of the genus *Lycopodium*. NEW PHYT., VII.,
1908, Text-figure 5.

a thin membrane which projects downwards from the stalk of the sporophyll and at its distal extremity bisects the dorsal lobe. An absolutely median radial section through the sporophyll would pass through this descending membrane and would thus not have a peltate form; sections on either side of the median line have the conformation figured, sometimes even while still including a portion of the vascular bundle, as in text-figure 5 of my paper. The descending membrane, as in *L. cernuum*, is left by mucilaginous degeneration in the lower portion of the stalk, only the epidermal layer remaining (Fig. 19, *mc*). Since the mature form is arrived at in this way in *L. inundatum*, it appears advisable to refrain from applying the term peltate to the sporophylls of this species. I did not use it reference to *L. inundatum* and I attempted to avoid it throughout my paper, since I do not consider that sporophylls such as those prevailing in this genus are strictly comparable with the truly peltate sporophylls of *Equisetum*, &c.

In *L. cernuum*, in addition to that portion of the dorsal lobe which, as in *L. inundatum*, *clavatum*, &c., is left by mucilagenous degeneration, Dr. Lang has described a small free flap (cf. Fig. 1, p. 358 of his paper). Since my examination of the sporangium-bearing organs of *Lycopodium* was practically confined to mature forms, I was unable to distinguish this differerence in development.

I understand that Dr. Lang refers only to this small free portion as the dorsal flap, whereas I, on the other hand, have so described the whole of that portion of the leaf-lamina which extends dorsally below the level of the sporophyll axis; the possession of this additional downgrowth appears to me to be but another instance of the greater complexity of the cone of this species. Both Dr. Lang and I have already laid stress on the conception that this greater complexity is correlated with the vertical approximation of the whorls of the sporangia.

The remarkably interesting results of a detailed comparison between the cones of *L. cernuum* and *Spencerites* by which Dr. Lang has once more drawn attention to the striking resemblance between these two forms seems to me another strong argument in favour of the primitive position of this species in the genus *Lycopodium*; I still consider "the *L. inundatum* type of cone reduced from that of *L. cernuum*"[1] and intermediate in position between the latter and simpler species of the genus. The argument on page 54 of my paper concerns the arrangement of the mature

[1] Lang, W. H., l.c., p. 363 (footnote).

sporophylls in the various species, and is not affected by their mode of development.

I have cordially to thank Dr. Lang for his courtesy in explaining to me his position and for the trouble he has taken in examining a specimen and slide of *L. inundatum* which I sent him in verification of my results.

Botany School,   M. G. SYKES.
      Cambridge.

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SUPPLEMENTARY NOTE ON THE ANATOMY OF
SAXEGOTHÆA CONSPICUA, LINDL.

WHEN a note on this subject was published a short time ago,[1] I was unfortunately unaware of a paper by Norén[2] published some time previously, dealing mainly with the structure and development of the pollen and nucellus, and with the mode of pollination of *Saxegothæa*. From his observations Norén concludes that the Araucarieæ and Podocarpeæ are related through *Saxegothæa*, a view that I was led to put forward from considerations of the anatomy of the latter.

[1] NEW PHYTOLOGIST, Vol. VII., p. 209, 1908.

[2] Norén, C. O. Zur Kenntnis der Entwicklung von *Saxegothæa conspicua*, Lindl. Svensk Botanisk Tidskrift, Bd. 2, p. 101, 1908.

Botany School,   W. STILES.
      Cambridge,
March 19th, 1909.

NOTES ON RECENT LITERATURE.

CYTOLOGY.

THE MODE OF PAIRING OF CHROMOSOMES

IN MEIOSIS.

THE remarkably constant and characteristic phenomena associated with the reduction division in plants and animals, have long attracted attention, and the interpretations which have been suggested have been many and various. But whereas formerly these inter-pretations might be divided roughly into two groups, respectively affirming and denying the existence of a true reduction involving the qualitative sorting out of chromatin elements, the scene of the controversy has now shifted. It is now generally admitted that a qualitative separation does take place in the heterotypic division (or at any rate in one of the two divisions of the meiotic phase), but there is no such harmony as to the manner in which it is supposed that this end is attained. In the earlier form of the controversy attention was centred mainly on the observation of the changes involved in the actual heterotypic division, that is to say, on the late prophase and metaphase of this division; it is now recognized that the true interpretation must rest on an accurate knowledge of the precise changes which take place at an earlier stage—the earliest stages of prophase.

Broadly speaking, two interpretations of the phenomena hold the field at the present day. The one, which can probably claim the greater number of supporters, involves the idea of a lateral pairing of the chromosomes, brought about by the approximation towards one another of two previously independent spireme threads, which are generally assumed to be derived respectively from the male and female germ-nuclei which united in fertilization. These two threads arrange themselves, during early prophase of the heterotypic division, or in some cases earlier, in parallel, becoming more and more closely approximated, until, at about the time of synapsis, a more or less complete, though temporary, fusion between the two takes place. From the contracted condition of the spireme characteristic of synapsis, there emerges a thread showing sooner or later distinct traces of its double origin. This double thread gives rise to the "bivalent" chromosomes of the heterotypic division, that is to say, to pairs of somatic chromosomes which lie side by side, having been brought into this position by the approximation of the threads towards one another, which took place during prophase. The heterotype division consists in the separation from one another of the two members of each pair of chromosomes, one member passing to the one daughter nucleus, its fellow to the other. This process of separation takes place throughout the whole series of pairs of chromosomes, and thus a qualitative reduction is brought about, each of the daughter nuclei containing a single series of

chromosomes, as compared with the paired or double series which is found in the somatic cells.

The alternative interpretation provides the same final result, but involves a different method of pairing. It is a characteristic feature of the heterotype division, that the spireme, as it emerges from the contracted condition known as synapsis, is thrown into a series of loops. According to the interpretation we are now considering, the pairing of the chromosomes is brought about by the approximation towards one another of the limbs of these loops. Thus each pair of chromosomes is at first a U-shaped structure, the two chromosomes being joined end to end, the point of junction forming the bent portion of the U. The two parallel limbs of the U come closer and closer together, and sooner or later a transverse fission takes place at the angle, the paired chromosomes now lying side by side, ready for the separation which takes place in metaphase of the heterotype division. It must be noticed that this method of attaining the paired arrangement,—by the looping of the thread and the subsequent approximation of the limbs of the loops towards one another—involves an "end-to-end pairing" of the chromosomes. Since the loops are generally continuous with one another at their inner ends, it follows that the chromosomes are arranged at this stage in a single linear series. Although direct proof is necessarily lacking, the evidence is very strong in favour of the correctness of the hypothesis that the two chromosomes which are united in each pair are respectively of maternal and paternal origin; it therefore follows that in the looped thread, as it emerges from its contracted state, chromosomes of maternal and paternal origin must be arranged alternately in a single linear series.

This is the essential point of difference between the two views, for the one described first implies that the maternal and paternal chromosomes are arranged in two independent series, "lateral pairing" being brought about by the arrangement of the two threads parallel to one another, followed by an approximation which becomes so close (during or shortly after synapsis) that it amounts to a temporary fusion.

At first sight it would appear to be a simple matter to decide between the claims of the two views; for if the former is correct and the pairing is essentially lateral, the loops into which the spireme is thrown after synapsis should show signs of their origin from paired threads, in other words they should be double structures. In the majority of cases they can clearly be seen to be double; but this double appearance is explained, by the supporters of the end-to-end pairing, as being due to the precocious longitudinal fission of the thread in preparation for the *second* maturation division.[1]

[1] It should be explained that this fission is described by all observers as taking place very early—at the latest it becomes apparent in the metaphase of the first division. Farmer and Moore look upon the heterotype division as "the intercalation of a special form of chromosome-distribution during the course of what otherwise would not differ materially from an ordinary pre-meiotic mitosis." (Quart. Journ. Microsc. Science **48**, 1905, p. 548), and thus account for the fact that the longitudinal fission which prepares for the second mitosis has already appeared, before the intercalated mitosis is complete.

A further factor, which has undoubtedly been the source of much of the disagreement between the views of various writers, lies in the difficulty of seriation of the various stages. The main outlines of mitosis have been followed in the living cell, but for the details it is necessary to work with fixed material. In the earliest stages of the meiotic phase considerable growth in size of the nuclei takes place, but in the later stages this ceases and correct seriation can only be arrived at by close study of a very large number of preparations. It seems to be clear that stages which are looked upon by those who advocate the one view as being early, are placed later in the series by those who hold the alternative interpretation, and conversely.

In a recent number of the Annals of Botany, Overton[1] has published a most interesting contribution to the subject. The additional evidence which he now brings forward certainly gives very strong support to the views put forward at an earlier time by him in conjunction with Strasburger, Allen and Miyake,[2] when the occurrence of a lateral pairing in the prophase of the heterotype division was advocated.

As has been explained, the two threads which take part in this pairing are looked upon as respectively derived from the male and female gametes, which by their union gave rise to the zygote from which the plant has been developed. This being so, it would be natural to expect that in some species indications of the pairing of the threads might be found at an earlier stage in the life of the plant than that immediately prior to the formation of the germ-cells. Such cases would form a continuation of the series, which, starting for example with the Uredineæ, where the two germ-nuclei remain quite distinct for the greater part of the life of the zygotic mycelium (2 X generation), includes forms like *Cyclops* and other Copepoda (in which, as Haecker and Reukert have shown, the maternal and paternal chromosomes form distinct groups, at any rate throughout the earlier mitoses of the individual), and has found its end terms in those numerous cases in which the union of the nuclei of the two germ-cells, at fertilization, is so close that, even in the first mitoses of the zygote, the maternal and paternal chromatin is already completely intermingled. Among such types as would be included under this last head, one might expect to find some in which the orderly pairing of the maternal and paternal chromatin does not take place until late in the life of the individual—not in fact until the onset of meiosis; and others in which the orderly arrangement of the parental chromatin begins at an earlier stage in the life of the individual. In the latter case, such an arrangement might manifest itself through a tendency toward the association of the chromosomes in pairs in the dividing nuclei of the somatic cells, or through the existence of parallel paired threads in the resting nuclei.

It may be said at once that the double structure shown by the primordia of the chromosomes, during the prophase of division in the pre-meiotic cells of the Cockroach, has been ascribed by Farmer

[1] "On the Organisation of the Nuclei in Pollen Mother-cells of Certain Plants." Ann. Bot., XXIII., 1909, p. 19.

[2] "Histologische Beiträge zur Vererbungsfrage." Jahrb. Wiss. Bot. XLII., 1905, p. 1.

and Moore,[1] not to an association of the chromosomes in pairs, but to the fission of the single chromosomes in preparation for the mitosis.

On the other hand, Cannon[2] found indications of the association in pairs of the chromosomes during anaphase of the somatic divisions of *Pisum*. Strasburger has found a similar association in *Pisum*[3] during metaphase, in *Galtonia* and in *Funkia*.[4] In the last genus the chromosomes are of different sizes, and Miss Sykes[5] has recently confirmed Strasburger's observation that chromosomes of similar size are associated with one another in the somatic mitoses, as is also the case, of course, in the heterotype division. Overton[6] has found the paired arrangement also in the cells of the root-tips of *Calycanthus*.

Unless some very fundamental mistake has been made in the observations, it is difficult to see how any interpretation based on the lines of that given by Farmer and Moore in the case of the Cockroach can be made to apply to such an association of chromosomes in pairs in metaphase and telophase. And if such an association exists, it is to be expected that indications of it would remain when the associated chromosomes become transformed into the threads of the resting nuclei. The paired arrangement of the threads which Miss Sykes[7] has described in the nuclei of *Funkia*, *Pisum*, *Hydrocharis*, *Lychnis* and *Bryonia* is, to say the least, suggestive in regard to this point.

In the majority of plants and animals the limits of the individual chromosomes are lost in the evenly distributed alveolar or reticulate framework to which they give rise in the resting nucleus, and their inter-relations are therefore so much the more difficult to trace. In 1905, Overton[8] presented evidence that the chromosomes persist as recognizable individual structures in the germ-cells of certain plants.[9] To these structures he gave the name of "prochromosomes." His last paper[10] includes some most important extensions of his earlier work upon these bodies, by whose means he is able to trace the relations of the chromosomes one to another, not only in the germ-cells, but throughout the various conditions of rest and division through which the somatic nuclei pass.

He finds that, in *Calycanthus* and *Thalictrum*, the prochromosomes of the somatic cells are arranged in pairs, connected with one another in series by parallel threads of linin, so that in the

[1] Q. J. M. S. **48**, 1905, pp. 528-537.

[2] Bull. Torrey Bot. Club **30**, 1903, pp. 519-543.

[3] Jahrb. Wiss. Bot., XLIV., 1907, p. 489.

[4] Ibid, XLII., 1905, p. 19.

[5] Arch. Zellforsch **1**, 1908, p. 392.

[6] Ann. Bot., XXXIX., 1909, p. 45.

[7] Op. cit.

[8] Jahrb. Wiss. Bot., XLII., 1905, pp. 121-151.

[9] See also Rosenberg: *Flora*, XCIII., 1904, p. 250. In the paper referred to below (page 39), Overton gives a list of plants in which prochromosomes, or corresponding structures, are known to occur. To this list may be added *Mercurialis*.

[10] "On the Organisation of the Nuclei in the Pollen Mother-Cells of Certain Plants." Ann. Bot., XXXIX., 1909, pp. 19-53.

resting nucleus of the somatic cells, two parallel spireme threads can be recognized. These two threads run through a reticulate framework consisting of fine threads, probably of linin, which contain no chromatin and have not been observed to connect with the spireme threads (Op. cit., p. 22). Similar structures with a similar arrangement are found in the nuclei of the germ-cells of *Richardia*, though in this plant the parallel arrangement of the connecting filaments of linin is not so easily made out. During the prophases of the heterotype division these parallel spireme threads become more distinct, the synaptic contraction occurs, and shortly afterwads the closest approximation of the parallel bodies to one another takes place. That is to say, the pairing of chromosomes, which is characteristic of the heterotype division, is already foreshadowed in the paired arrangement of the chromosomes in the somatic cells of these plants.

As Overton says, it is not easy to see how such observations can be related to a method of pairing, brought about by the folding of a thread into a series of loops. The later stages of the preparation for the heterotype division might be susceptible of interpretation on this view, but the earlier stages and the somatic nuclei, as described by Overton, are something of a stumbling block. In the search for a correct interpretation of the phenomena involved in the heterotype division, the point upon which attention has been especially concentrated has been shifted from the late prophase and metaphase to the earliest prophase; are we to find the answer in a stage earlier still—in the structure of the somatic nuclei ?

We have still to reckon, however, with Farmer and Moore's observations upon *Periplaneta.*[1] As has been mentioned, in the pre-meiotic nuclei of this genus, double structures appear, which, as a comparison of the figures will show, are very like the paired prochromosomes described by Overton. Farmer and Moore look upon these as the "Anlagen" of single chromosomes, in which the longitudinal fission appears thus early in the prophase of the division, and they give a description of the prophase of the heterotype division which differs fundamentally from that of Overton. They find that in this division, instead of the chromosomes making their appearance in the form of thirty-two split rods, as they do in the pre-meiotic mitoses, the spireme thread segments into about half as many lengths (which of course represent pairs of somatic chromosomes joined end to end). These lengths are bent round upon themselves in the form of loops or rings; the loops break across the curved portion and give rise to the pairs of chromosomes which now lie side by side.

Although some of the stages figured by Farmer and Moore, in the prophase of the heterotype division, do not find any quite exact parallel in Overton's figures of *Thalictrum* and *Calycanthus*, the divergence of opinion is no doubt primarily connected with the different interpretations put upon the double structures found in the pre-meiotic divisions. According to Farmer and Moore the number of these double structures would be the same as that of the somatic chromosomes; according to Overton each double body consists of the primordia of a pair of somatic chromosomes. The

great difficulty of coming to an exact determination upon this point is emphasized by the fact that in his last paper, Overton gives the number of chromosomes in *Thalictrum purpurascens* as forty-eight —twice as many as the number indicated by Strasburger,[1] and by Overton himself in his earlier paper when he " mistook the pairs of chromosomes for a single chromosome."

For a detailed discussion on the permanence of chromosomes, the double nature of the somatic nucleus, and the conjugation between pairs of chromosomes in the prophase of the heterotype division, the reader must be referred to Overton's paper. Cytologists will be grateful for the excellent summary of the literature upon these subjects which is also given.

One feels that in the study of forms such as those described by Overton, where the chromosomes can be traced individually throughout all conditions of the nucleus, lies the most promise for the elucidation of the manner in which the pairing of the chromosomes takes place. One of the main objects of work of this kind, as is very clearly shown by the general trend of the discussions given by each author, is the attempt to find a satisfactory cytological basis for the segregation of characters which is known to take place in (or prior to) the formation of the germ-cells in many plants and animals. The pairing of homologous chromosomes, and their separation in the heterotype division, affords the promise of a solution, but while we find two theories arriving at this desirable end by such dissimilar routes, it is not altogether surprising that the sceptic persists in his unbelief.

Indeed, in the absence of evidence more definitely connecting the chromatin with the hypothetical material particles (pangens) whose existence has been postulated in order to explain the transmission of inherited characters, and with the exception of the remarkable facts brought to light by the observations of Wilson and others upon the determination of sex in the Hemiptera, etc., almost the strongest presumption in favour of the significance usually attributed to the heterotype division, lies in the change of symmetry which takes place in the divisions of the nuclei at that point. In the somatic cells there exists one form of symmetry, in that each of the chromosomes undergoes a longitudinal fission, and the daughter nuclei are, therefore, so far as our knowledge goes, qualitatively exactly similar to one another and to the parent nucleus from which they originated. In the heterotype division another type of symmetry supervenes, in that the chromosomes become associated in pairs and each daughter nucleus receives one member from each pair. Each daughter nucleus therefore receives a single series of chromosomes which are individually and collectively homologous, but not necessarily identical in quality, with those of the sister nucleus.

This change of symmetry corresponds exactly with that which the results of experimental work demand. The facts of regeneration show that, in general, the various regions of the soma of a plant retain the potentiality for the development of all the characters proper to the plant; translated into terms of material particles or pangens, this means that the pangens have been distributed

[1] Sitzber. Akad. Wiss. Berlin, XVIII., 1904, p. 604.

symmetrically during the cell divisions, in such a way that each cell has received a complete series of pangens. But this method of symmetrical distribution is replaced by a new plan of symmetry in the formation of the germ-cells, such that, to take the case of a simple di-hybrid in which segregation is complete, one half of the germ-cells are of one kind, the other half of another kind, and each kind is pure in respect of the character which it bears. As Bateson[1] has said, this symmetrical arrangement can only be regarded as a consequence of some numerical symmetry in the cell-divisions of gametogenesis. But the symmetry is of a different kind from that which extends over the somatic cells; the change of symmetry which cytological studies have shown to occur in the heterotype division is just such an one as is required to meet the case, and it occurs, in all probability universally, wherever sexual reproduction occurs. In spite of all the difficulties of directly identifying the nucleus as the carrier of inherited characters, it is hard to believe that such a parallel can be a mere coincidence, and without significance in the distribution of the characters to the gametes.

But whatever weight may be attached to such a parallel as this, it amounts at the best to nothing more than a presumption; what is required to substantiate modern views on the significance of the heterotype division, is evidence which will definitely connect the nucleus with the transmission of inherited characters. Until that has been provided much that has been written and said, more especially with regard to the details of the hypotheses, belongs to the realms of pure speculation. The cytological study of pure races and hybrids, which show partial or total sterility,[2] has scarcely realized the hopes which were entertained of acquiring direct evidence. In the majority of such cases the sterility cannot be referred directly to abnormalities occurring in the nucleus itself, either in the condition of rest or of division. A very hopeful field however is opened out by the study of races in which new types are being thrown off, as in the species of *Oenothera*, which have been examined by Gates,[3] Miss Lutz[4] and Geerts.[5] Gates has found that the pairing between the chromosomes in the heterotype division does not always take place; this allows irregularities in the distribution

[1] Brit. Ass. Rep., 1904, p. 583.

[2] A general review of this subject has recently been given by Tischler in the *Arch. Zellforsch.*, **1**, 1908, pp. 33-151.

[3] *(a)* "Pollen development in hybrids of *Oenothera lata* and *O. Lamarckiana*." Bot. Gaz., **43**, 1907, p. 81.

　　(b) "Hybridization and Germ-Cells of *Oenothera* mutants." Ibid. **44**, 1907, p. 1.

　　(c) "The Chromosomes of *Oenothera*." Science, N.S. XXVII., 1908, p. 193.

　　(d) "A Study of Reduction in *Oenothera rubrinervis*." Bot. Gaz., **46**, 1908, p. 1.

[4] "Chromosomes of the Somatic Cells of the *Oenotheras*." Science, N.S. XXVII., 1908, p. 335.

[5] *(a)* "Ueber die Zahl der Chromosomen von *Oenothera Lamarckiana*." Ber. d. D. Bot. Ges., **25**, 1907, p. 191.

　　(b) "Beiträge zur Kenntniss der cytologische Entwicklung von *Oenothera Lamarckiana*." Ibid, **26a**, 1908, p. 608.

of the chromosomes which takes place at that division, so that occasionally both members of one pair of chromosomes may pass to one daughter nucleus, leaving the sister nucleus without a representative of that pair. Germ-cells will thus arise lacking certain of the chromosomes which are present in the parental type. On the hypothesis that the development of certain characters is determined by the presence of corresponding chromatic substance, such irregularities in the distribution of the chromosomes would account for a certain class of mutation, which takes the form of the loss of a character which is present in the parental type. The giant *Oenothera gigas* belongs, however, to another class of mutation, in that it possesses twenty-eight chromosomes in the somatic cells and fourteen in the reduced cells, as compared with the fourteen and seven chromosomes which occur in the corresponding cells of the parent type, *O. Lamarckiana.*

A further most interesting point is brought to light by Gates' observations[1] on the hybrid between *O. gigas* with a form known as *O. lata* which has the same number of chromosomes as *O. Lamarckiana.* The hybrid has of course twenty-one chromosomes. In the heterotype division these are distributed ten to one pole, eleven to the other. This method of distribution is different from that which obtains in the hybrid between *Drosera rotundifolia* ($2X=20$; $X=10$) and *D. longifolia* ($2X=40$; $X=20$). The hybrid has $(10 + 20)= 30$ chromosomes; Rosenberg[2] has shown that in the reduction division, there are ten pairs of chromosomes and ten single chromosomes. In all probability this must be interpreted as meaning that ten of the *langifolia* chromosomes have paired with the ten *rotundifolia* chromosomes, and will separate at metaphase; the remaining ten *longifolia* chromosomes do not pair, and are distributed somewhat irregularly between the daughter nuclei, or may be left behind in the cytoplasm. In the *Oenothera* hybrid on the other hand, the distribution is such as to suggest that pairing does take place among six of the seven *gigas* chromosomes, which are unable to find fellows in the series contributed by the other parent, the odd chromosome passing to one pole or the other according to chance. The hybrid produces pollen in abundance and the results of further experiments and observations upon the posterity of the hybrid will be looked forward to with great interest.

R.P.G.

[1] "The Chromosomes of *Oenothera*." Science, N.S. XXVII., 1908, p. 193.

[2] Ber. d. D. Bot. Ges., XXII., 1904, p. 47.

FOSSIL PLANTS.

M. PAUL BERTRAND ON THE STEMS BELONGING

TO *CLEPSYDROPSIS.*

LAST November M. Paul Bertrand published a short report in the "Comptes Rendus de l'Académie des Sciences" on the stems belonging to *Clepsydropsis*, a genus of Unger's revived for certain petioles hitherto supposed to be distinctly Botryopteridean. The best known species of *Clepsydropsis* is probably that described as *Rachiopteris duplex* by Williamson. The vascular bundle of this petiole is shaped like an hour-glass; the species is sometimes included in the genus *Zygopteris*, the two swollen ends of the hour-glass representing thickened side-pieces of the H-shaped trace of that genus. It is, therefore, very interesting that M. Paul Bertrand, from a careful comparison of the petiolar bundles of *Clepsydropsis* with the structure of the stem at the departure of the trace in *Cladoxylon* and in *Medullosa* (*Steloxylon*) *Ludwigi*, should have come to the conclusion that the first-mentioned genus represents the petioles of the two latter forms. In the case of *Medullosa* (*Steloxylon*) *Ludwigi* such a view is supported by the association of this type of stem with *Clepsydropsis Kirgisica.*

These fossils from the Lower Culm are of great antiquity, and without necessarily accepting M. Paul Bertrand's view that *Clepsydropsis* appears to be very primitive, and "infinitely closer than any other plant as yet described" to a form in which Lycopods, Ferns and Medulloseæ ultimately converge, it is obvious that the discovery that Botryopteridean petioles were associated with stems included in the Cycadofilices on account of their anatomy is very remarkable. The significance of this circumstance is enhanced by the similarity (recognized as early as 1881 by Dawson) between *Cladoxylon* and *Asterochlaena* (his *Asteropteris*), and by the fact that *Botrychioxylon*, regarded as one of the Botryopterideæ, possessed a considerable amount of secondary xylem.[1]

A certain number of Cycadofilicinean stems are now known to have belonged to seed-bearing plants and suspicion has fallen on many others. As other Medulloseæ were certainly Pteridosperms, some doubt is naturally cast upon the cryptogamic nature of *Medullosa* (*Steloxylon*) *Ludwigi*, although this species is not a true or typical *Medullosa*. But as its petioles and those of *Cladoxylon* appear to belong to the same "genus" (*Clepsydropsis*), *Cladoxylon* itself may turn out to be a Pteridosperm, although further and more direct evidence would be wanted to confirm the suspicion. Further the reference of *Clepsydropsis* to Cycadofilicinean stems throws some doubt on the cryptogamic nature of the Botryopterideæ, now frequently regarded as the most important Palæozoic group of "Ferns".[1] This doubt must rest at least on the Zygptereæ (to

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[1] D. H. Scott. "Studies in Fossil Botany." Second Edition, Vol. I., 1908.

which *Clepsydropsis* belongs), the more complex, and so for as we know, the older of the two families included in the Botryopterideæ. For these reasons M. Paul Bertrand's researches seem to be of great importance.

ISABEL BROWNE.

FUNGI.

"Synopsis of the British Basidiomycetes." A descriptive Catalogue of the drawings and specimens in the Department of Botany, British Museum; by Worthington George Smith, F.L.S. Printed by order of the Trustees of the British Museum.

THIS book is a welcome addition to the Fungus-floras of this country. In it the author embodies the notes of many years made on the characters and distribution of the higher Basidiomycetes. The scheme of classification generally adopted is that used by Fries in his Hymenomycetes Europæi (1874), but the sub-genera of *Agaricus*, e.g., *Amanita*, *Collybia*, etc., used by Fries, are raised to the rank of genera, as is now indeed customary. The number of such genera is increased by the addition of *Amanitopsis*, *Hiatula* and *Togaria*. The genus *Exobasidium*, parasitic on species of *Vaccinium*, is still kept in the Thelephoraceæ, but it would seem better to assign it to a distinct group, as is done in Engler's "Pflanzenfamilien." It will be noted also that the anomalous genus *Tremellodon* is placed in the Hydnaceæ, whereas Massee assigns it to the Tremellineæ on account of its divided basidia and gelatinous consistency.

The descriptions of species in this book certainly do not err on the side of excessive length. Indeed it must be admitted that such brevity as is prevalent here will make it difficult for a beginner to be certain that his determination of species in all cases is correct. It will probably be found that he will be obliged to combine the use of this book with that of larger floras. On the other hand such long descriptions as are to be found in some other books are not desirable.

An attempt has been made to give somewhat more definite details of habitats than have been customary in former mycological floras, though it must be said that a good deal yet remains to be done in this respect. The general term "woods" is still often used as descriptive of the habitat of many of these fungi, whereas one would like to know what kind or kinds of wood are really indicated. The ecological distribution of the higher Fungi is now more widely recognised than formerly, and one looks forward to the time when a "biological" flora of the Basidiomycetes can be written.

The author of this synopsis has thoughtfully provided a glossary of special mycological terms. This will be appreciated by the

beginner, who is often at a loss to know what is the significance of some of the terms used by the systematists of this group.

The text-figures are admirably prepared, and it was a happy conception to include plates at the end of the book in order to shew the relationships between those genera of the Agaricaceæ which differ in spore-colour, but whose general anatomy is the same. The letterpress of the book is excellent and the misprints are insignificant in number.

It may be added that the nomenclature is in accordance with the Vienna Code of Rules already applied to the nomenclature of vascular plants. The question of the authorities for the species-name of non-vascular plants is to be brought up at the International Congress in 1910, but it is unlikely that it will differ greatly from the code adopted for the higher plants.

F.T.B.
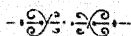
RECENT ADVANCES IN THE STUDY OF HEREDITY.

(A Course of Lectures, for the University of London, delivered in the
Summer Term, 1909).

By A. D. Darbishire.

LECTURE I.

On the Changes which have taken place in our
Conception of the Relation between successive
Generations of Organisms.

WHEN I first undertook to give this course of lectures I
endeavoured, in planning the subject-matter to be dealt
with, to confine myself strictly within the limits prescribed by the
title of the course, "*Recent* Advances in the Study of Heredity";
but I soon found that it was impossible to explain the full interest
and significance of recent work if the theories which are now
receiving general credence were not considered in relation to those
which preceded them.

I therefore propose in this first lecture to trace, in outline, the
history of the phases through which the problem of inheritance has
passed.

Moreover, it seems to me that it is only by travelling over
again, as swiftly as may be, the tracks which have led us to the
points we have now reached that we can see how the land lies and
thus obtain some idea of the directions in which present methods
of investigation are leading us.

I further submit that if we attack the subject as if it were a
living and growing organism we shall attain to a truer conception of
our relation to the phenomena which we are investigating than we
should do if we shut our eyes to everything that has happened before,
or may happen after, a narrow strip of time.

The statement, with regard to any set of opinions, that we know what they are, but know not what they may be, can only be made by those who cannot see, or are too lazy to face, the real truth; which is that we know not what they are until we know what they have been and that it is only when we thus know what they are, that we are in a position to know what they may be.

The history of the study of inheritance may be divided into three periods, which roughly correspond with the end of the 18th, the latter half (if not the whole) of the 19th, and the beginning of the 20th centuries. Speculation in the first period, started off on a track which was remarkably like that which we now follow and consider to be the right one; it went astray during the second period and the stagnation which characterizes that period is due to the misapprehension of the nature of the problem, which prevailed during it. The third period is characterized by a return to the path which, we believe, will lead us, and indeed, in great part, already has led us, to an understanding of the nature, and ultimately to a solution, of the problem.

THE FIRST PERIOD.

The saying that a little knowledge is a dangerous thing is a very profound one, and is illustrated in a remarkable way by the history of the attempts to deal with the problem of inheritance. Thus, for a man coming to close quarters with a natural problem it is better that he should either know hardly anything at all about it or a very great deal; what is almost certain to be fatal to a successful grappling with the problem is an intermediate amount of knowledge. If he knows hardly anything at all, it is possible or even likely that, if he is keenly perceptive, he may get a general conspectus of the most salient features of the problem which will lead him to an interpretation of it, which is not far from the truth. But if he knows more than this, through having paid close attention to one feature, the knowledge which he has looms too large in proportion to its value, and is dust in his eyes which prevents him from obtaining the general conspectus. Suppose there are twelve essential features of the problem; it is better to see each one dimly, than to see two so brightly that the rest are in darkness. (Best of all, of course, is to see all brightly. But this is very rarely attained to). Thus it is that the poetical imagination of Erasmus Darwin perceived the problem of inheritance in the same

light as that in which it appears to us now, whilst his scientific successors misapprehended it.

Section XXXIX, "Of Generation," of Erasmus Darwin's Zoonomia begins with the following words.[1] "The ingenious Dr. Hartley, in his work on man, and some other philosophers have been of opinion, that our immortal part acquires during this life certain habits of action or of sentiment which become forever indissoluble, continuing after death in a future state of existence; and add that if these habits are of the malevolent kind, they must render their possessor miserable even in Heaven. I would apply this ingenious idea to the generation or production of the embryon or new animal, which partakes so much of the form and propensities of its parent."

"Owing to the imperfection of language the offspring is termed a *new*[2] animal, but is in truth a branch or elongation of the parent, since a part of the embryon-animal is, or was, a part of the parent, and therefore in strict language, cannot be said to be entirely *new* at the time of its production; and therefore it may retain some of the habits of the parent-system.

"At the earliest period of its existence the embryon would seem to consist of a living filament with certain capabilities of irritation, sensation, volition and association, and also with some acquired habits or propensities peculiar to the parents; the former of these are in common with other animals; the latter seem to distinguish or produce the kind of animal, whether man or quadruped, with the similarity of feature or form of the parent."

This is a most remarkable prevision of the idea embodied in Butler's doctrine of oneness of personality of individuals in successive generations and in Weismann's doctrine of the continuity of the germ-plasm. According to Erasmus Darwin the germ, or living filament, starts with the peculiarities which distinguish the organism into which it will develop; and the question how those peculiarities got there, does not present itself to him as *the* outstanding difficulty as it did to Charles Darwin.

The causes which brought about the stagnation—nay retrogression—in the study of inheritance during the 19th century are not easy to disentangle; it is therefore with some diffidence that I make the following suggestions and I do not wish to be understood

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[1] London (1794-1796). I am indebted for my acquaintance with this passage to Samuel Butler's "Evolution, Old and New."

[2] The italics are Darwin's; Butler prints the whole of the second paragraph in italics.

as doing any more than submitting them to your consideration. But before I do so I should like to answer an objection which some among you may have been inclined to bring against my chronological delimitation of the three periods into which I have divided the history of the study of inheritance. You may object that the third period begins with the publication of Weismann's Continuity of the Germ-Plasm in 1885, or Butler's Life and Habit in 1877 or Mendel's *Versuche über Pflanzen-hybriden* in 1865. This is not my meaning. By saying that during the 19th century investigation and speculation proceeded along wrong lines I do not mean that workers and thinkers who were on the right track did not exist during that period; but that the mass of biological opinion was on the wrong track. In fact my meaning cannot be better illustrated than by reference to the fact that the work of the three men who did most to bring about the return to the right track (Mendel, Butler, and Weismann— I give their names in the order of the appearance of their most important works) although done roughly between 1860 and 1890, has not been understood and appreciated until recent years. I shall show, later on, that the work of Weismann is not, as it may at first sight appear to be, an exception to this statement.

THE SECOND PERIOD.

The great difference in the state of opinion between the age in which Erasmus and that in which Charles Darwin lived, was that the latter had succeeded, where his grandfather and Lamarck had failed, in convincing the intelligent public that the diversity of organic forms which people the earth had been brought about by a process of descent with modification. This in itself would not have made much difference. It is the theory advanced to account for this process which has had such a profound effect on the theory of inheritance.

A theory of evolution having been established, two ways of accounting for the manner in which new characters arise and persist, were possible. The new character could arise either in the mature organism or in the germ which gave rise to it. Darwin chose the former alternative; which made it necessary for him to put forward a theory to account for the manner in which the newly arisen character could be so impressed on the germ that it would be reproduced in the next generation. The theory which Darwin suggested was that of Pangenesis, which can be found in "Animals

and Plants under Domestication." The theory of Pangenesis commits Charles Darwin to a conception of the relation between successive generations of organisms, in which the soma occupies a primary and foremost position, inasmuch as Darwin starts with the soma, and directs his theory to the solution of the problem how the characters of an organism get into the germ-cells which it produces. The subordinate position which the germ occupies in Charles Darwin's theory may be expressed by the statement that according to him the egg is the means or channel whereby one hen produces another. The subordinate position which the soma occupies in the conception of inheritance which we believe to be true to-day may be expressed by the saying, which Butler quotes, that a hen is merely an egg's way of producing another egg. The modern view (see The Third Period, p. 163) is also expressed by Michael Foster in the opening paragraph of the Chapter on Death in the fourth edition of his text-book of Physiology which was published in 1884, a year before the publication of Weismann's Continuity of the Germ-Plasm. "When the animal kingdom is surveyed from a broad standpoint, it becomes obvious that the ovum, or its correlative the spermatozoon, is the goal of an individual existence : that life is a cycle beginning in an ovum and coming round to an ovum again. The greater part of the actions which, looking from a near point of view at the higher animals alone, we are apt to consider as eminently the purposes for which animals come into existence, when viewed from the distant outlook whence the whole living world is surveyed, fade away into the likeness of the mere by-play of ovum-bearing organisms. The animal-body is in reality a vehicle for ova ; and after the life of the parent has become potentially renewed in the offspring, the body remains as a cast-off envelope whose future is but to die."

I have laid especial emphasis on the fact that Darwin in his theory of inheritance started with the soma and sought to explain how its characters were impressed on the germ-cells which it carries, because this fact has influenced the history of the interpretation of heredity far more profoundly than is commonly recognized. The theory of heredity which was almost universally, though tacitly, held by naturalists and breeders during the last decades of the 19th century owes its essential features to Darwin's " somatic " view of the matter. This theory was that the characters of a given generation were determined, in a diminishing degree as the progenitors became more remote, by the characters of their parents, grandparents,

great-grandparents, and so back. I propose to call this theory, for convenience of reference, "The Theory of Ancestral Contributions." [1]

It follows from this theory that our ability to predict the result of a given mating depends on the extent of our knowledge of the ancestry, *i.e.*, the somatic characters of the ancestors of the two forms mated. The attempt, which stands in such sharp contrast to the Mendelian method of procedure, "to breed out" an undesirable characteristic by breeding for many generations from individuals which do not manifest it, is based on a deeply rooted, though perhaps not definitely formulated, belief in this theory. The delusion that by breeding for a sufficiently large number of generations from an Andalusian Fowl (known now to be a hybrid form which will *always* throw blacks and "splashed-whites" in definite proportions) it will ultimately be possible to obtain a race of pure Andalusians, can only be due to a belief that the characters of offspring are determined by the somatic characters of their parents and ancestors to a diminishing extent as we proceed backwards. And really it involves some such theory as Pangenesis to account for it. But the practical breeder is not primarily concerned with the interpretation of the phenomena he witnesses, or with the scientific basis on which the principles which he follows are founded; all he requires is a principle which shall guide him to the end to which he wishes to attain. There is, however, not much difference between the practical breeder and pure biologist in the matter of the attention which either pays to the scientific explanation of this theory; for the biologist is guilty of retaining a belief in the theory of ancestral contributions long after he has not merely formally given up his belief in the theory of Pangenesis, but after he has declared his allegiance to the principle involved in Weismann's doctrine of the continuity of the germ-plasm, namely that inheritance is not from soma to soma, but from germ to germ. It is, in my opinion, important to recognize the reality and universality of a belief in the theory of ancestral contributions, because this theory, which is merely another name for what is called the common

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[1] Whilst this lecture is going through the press, a paper, by Professor Pearson, entitled *The Theory of Ancestral Contributions in Heredity* has appeared (Proc. Roy. Soc., Series B, Vol. 81, p. 219). I shall deal with the point raised by the author in a later lecture, but should like to state here that whilst I am in substantial agreement with Professor Pearson's main contention, my "Theory of Ancestral Contributions" is a physiological theory of inheritance applicable to individuals, whilst the Law of Ancestry is a statistical generalization relating to masses, the component individuals of which mate at random.

sense view of the matter, is held all the more firmly and deeply because it is held to a large extent unconsciously. It "stands to reason" that if you go on breeding long enough from Andalusian fowls you will ultimately obtain a pure race of them.

It is important to recognize, so far as we can, the exact nature of the general theory of inheritance which directed speculation and practical breeding during the period preceding the revolution initiated by Weismann ; and this I have attempted to do by tracing it to that conception of inheritance (entertained dimly by Lamarck and definitely by Charles Darwin) which calls for some explanation of the mechanism by which the characters of an organism are impressed on the germ-cells which it contains.

THE THIRD PERIOD.

The revolution in opinion which may be said to consist in the perception that the answer to the question " which came first, the hen or the egg ?," is "the egg," was, as I have said, initiated by the publication of Weismann's theory of the continuity of the germ-plasm in 1885. The revolution has consisted in a swinging round of our point of view through 180 degrees. We no longer look from the soma to the germ, but from the germ to the soma. We no longer ask ourselves : how do the characters of an organism get into the germ-cells which it produces ? but, how are the characters of an organism represented in the germ-cells which produce it ? But though the majority of biologists do lip-service to Weismann's view of the matter, many of them retain, or have done until very recently, a belief in the theory of ancestral contributions, which is diametrically opposed to the Weismannian conception. Men's relation to new theories seems to me to have been always the same. They do not first take in a new theory and then announce their adhesion to it ; they first announce their adhesion to it and then gradually take it in. Indeed it is only now that people are beginning to believe that the characters of organisms are determined by the potentialities in the germ-cells which give rise to them, and not by the somatic characters of their parents or their ancestors.

That which has been most effective in converting biological opinion to this theory has been the body of fact and hypothesis which we owe to Mendel and those who have worked on the lines laid down by him. And it seems worth while to consider briefly the relation between Weismann and Mendel. It has been argued by

some critics of Mendelian activity that many of the new conceptions which are ascribed to Mendel are in reality due to Weismann. We may admit this to be perfectly true in the sense that the Mendelian discoveries have succeeded, where bare enunciation failed, in bringing home to us the truth of the view put forward by Weismann in 1885, without imputing to those who have worked on the foundations laid by Mendel any desire to claim anything for him which is not his. Nevertheless, in justice to Mendel, it is only right to point out that, although we first became familiar with the Weismannian conception from Weismann's lips in 1885, this conception must have been present to Mendel's mind in 1865 at the latest, inasmuch as the theory by which he sought to account for his results related solely to the contents of the particular germ-cells concerned in the production of each generation, and not to the parents or ancestors of that generation. If it is true, as some believe, that the Mendelian hypotheses would not have been accepted if Weismann had not prepared the way by insisting that attention should be fixed primarily on the germ, it is also true that Weismann's conception of inheritance would not have received the wide acceptance which it has if it had not been for the manner in which the Mendelian discoveries have brought it vividly home to men's minds.

The relative share which these two men have had in the advancement of our understanding of inheritance may further be expressed in the statement that whilst Weismann showed what the question to be answered, was—namely: how are the characters of an organism represented in the germ-cell which produces it?—Mendel invented the machinery by means of which an answer to it is being supplied.

I have laid this emphasis on the community of the object which both Mendel and Weismann were effective in forwarding, because it supports my thesis that the 19th century was characterized by the prevalence of a fog of misapprehension as to the true nature of the problem of inheritance, which the solitary efforts of the two men, not yet in co-operation, were powerless to disperse.

The identification of the ends towards which these two men were working also makes it possible to understand the result of the coming together of two men which is full of the deepest interest. This intercourse—it was a correspondence—took place between one of the foremost biologists composing that lower foggy stratum of thought which carried general biological opinion

with it, and one of the handful of men who were on the right track, who was unknown to biologists during his life-time. I refer to the correspondence between Nägeli and Mendel. Mendel first wrote to Nägeli with the object of procuring specimens of *Hieracium*: he sent him his paper and discussed fully the criticisms which Nägeli offered. If further evidence were needed that Mendel spared no pains in his attempt to explain his theory to Nägeli, it is to be found in the fact that he went to the trouble of putting up packets of peas illustrating his various gametic types, and sent them to Nägeli.

Now Nägeli was especially interested in the problems presented by heredity; but his attitude to it was almost identical with that of Charles Darwin. Was it to be wondered at then that he completely failed to understand the significance of Mendel's work? Such was the case; for when in 1884 he published his great treatise on heredity,[1] no reference was made to Mendel or his work. "That this neglect was due to want of comprehension" (I quote from Bateson's 'Mendel's Principles,' p. 55) "is evident from a passage where he describes an experiment or observation on cats, which as it happens gives a simple Mendelian result. The Angora character (recessive) disappeared in a cross with a certain common cat whose hair character is, as we know now, dominant. The cross-breds were mated together and the Angora character reappeared in one individual among a litter of common cats. This typically Mendelian fact was actually thus under Nägeli's own observation, but from the discussion which he devotes to the occurrence it is clear that Mendel's work must have wholly passed from his memory, having probably been dismissed as something too fanciful for serious consideration."

It will be gathered from what I have already said that the explanation which I should offer of Nägeli's inability to understand Mendel's work is that the two men were extreme representatives of the two diametrically opposite attitudes to the phenomenon of inheritance, on which I have already laid stress. Nägeli could not accept or understand Mendel's theory without recognizing that the problem to whose solution he had devoted so much of his life was an unreal one. How unreal the problem, as approached from Nägeli's and Charles Darwin's standpoint, appeared to Mendel can be gathered from the fact that so unconsciously certain was Mendel of the modern view that he does not stop to consider the opposite

[1] Mechanisch-physiologische Theorie der Abstammungslehre.

one. He bases his theory, straight away, on the assumption that the character of the peas in his various generations are determined solely by the potentialities latent in the germ cells which give rise to them, and that the character of their parents and grandparents having nothing to do with it. Nägeli, whose theory differed very little from Charles Darwin's Pangenesis, could not admit the truth of this assumption without also admitting that the particular problem he had devoted his energies to solve was a fictitious exercise which bore no relation to actuality. Few men are able, or, if able, willing to appreciate the significance of work which involves the stultification of their own.

The coming together of these two men, representative of these two diametrically opposed views, and their complete inability to understand one another, appears to me as one of the most romantic events in the history of biology.

Before I pass on to the demonstration of what may seem the least credible part of my thesis, namely that the Weismannian or germinal theory of inheritance was not fully perceived until it received the support of Mendel's discoveries, I wish to make it clear that I am not suggesting that this is the only revolution in opinion which these discoveries have brought about; and to explain that I have laid such stress on the part which these discoveries have played in completing this revolution because no attention has been paid to it hitherto.

The reason that those who have been engaged in the prosecution of Mendelian studies have made no reference to this part played by Mendel's own discoveries is not, in my opinion, that they would not admit that these discoveries have had this effect, but that they admit it so unreservedly and fully and unconsciously that to make any reference to it, even if it occurred to them to do so, would appear to them to be uttering what was merely a self-evident commonplace. But it should not be forgotten that these inferences appear with a much more vivid reality to those actually engaged in the investigation of natural phenomena than they do to those whose acquaintance with these phenomena is of necessity second-hand. By second-hand I do not mean that those of you who are not prosecuting such researches are condemned to come no closer to the phenomena than you can get by reading about them in books or hearing about them in lectures. Later on I shall show you specimens, illustrating many of the phenomena, which I have grown myself. You will see the results of the experiments. But

the difference between merely reading or hearing about the results and seeing them, is not much greater than the difference between seeing them, and planning and carrying out and laboriously recording the results of the experiment. I propose therefore to confine myself to the exhibition of such instances as you can easily make for yourselves in the course of a few years.

This, therefore, is my reason for laying such emphasis on the nature of the revolution in opinion which is now approaching completion. That this is the real turning point will not, I think, be denied. Without the recognition that all attempts to predict the results of a given mating based on a knowledge of the somatic character of the individuals mated and of their ancestors are futile, none of the progress made since the beginning of this century would have been possible. And it was only natural that, so long as the problem of inheritance which naturalists set themselves to solve was a fictitious one, no progress was made.

It was failure to recognize that one of the most, if not *the* most, essential features of Mendel's theory was that it was a germinal theory of inheritance (*i.e.*, a theory to account for the manner in which the characters of organisms are represented in the germ-cells which produce them) that rendered the first reception of this theory so hostile. I am thinking of the criticism of this theory by Weldon. He concluded his critique[1] with the words "The fundamental mistake which vitiates all work based upon Mendel's method is the neglect of ancestry, and the attempt to regard the whole effect upon offspring, produced by a particular parent, as due to the existence in the parent of particular structural characters; while the contradictory results obtained by those who have observed the offspring of parents apparently identical in certain characters show clearly enough that not only the parents themselves, but their race, that is their ancestry, must be taken into account before the result of pairing them can be predicted."

I think this sentence shows that the theory of inheritance in Weldon's mind was closely similar in essence to what I have called the theory of ancestral contributions, the theory, namely, that the characters of offspring are determined by the characters both of their parents and ancestors. We see, at any rate, that in Weldon's theory the *somatic* character of parents and ancestor are the data which enable us to to predict the characters of offspring. Whether

[1] *Biometrika*, I., p. 228.

or no, Weldon believed in the the theory of Pangenesis (which his view of inheritance in reality involves), in some form or another, I do not know. He was perpetually insisting that it was our business first to describe hereditary phenomena, and then, after this had been done, to attempt to account for them; so that I think that the answer he would have given, if asked, would have been that he considered that the time for interpretation was not yet come. But this is mere conjecture.

The essential point about Weldon's concluding sentence, which I desire to lay before you is this:—so entirely on the somatic "plane," if I may so express it, were his thoughts about inheritance that the antithesis between what he was attacking and what he was upholding did not appear to him as the antithesis between (*a*) the germinal theory of inheritance, which we associate with Weismann, and (*b*) the somatic theory of inheritance of Charles Darwin and Nägeli, but as the antithesis between (*a*) a theory of inheritance which takes the somatic characters of the parents *plus* those of a great number of the ancestors into account and (*b*) a theory which relates to the somatic characters of the parents alone; whereas, as I maintain, the basis on which the whole of the modern attempt to deal with the problem of heredity rests is the doctrine that the somatic characters both of the parents and of the remoter ancestors may be left out of account in the attempt to predict the result of a given mating, except, of course, so far as they afford an indication as to the nature of the gametes born by them. Bateson answers that part of Weldon's criticism which I have quoted in the following words " I should rather have said that it was from Mendel, first of all men, that we have learnt *not* to regard the effects produced upon offspring as due to the existence in the parent of particular structural characters. We have come rather to disregard the particular structure of the parent, except in so far as it may give us as a guide to the nature of the gametes." But this conception is identical with that which we associate with the name of Weismann. Let us not trouble about the trivial question as to whose name we shall associate it with. Let us call it the germinal theory of inheritance, and note that it occurred independently to Mendel and Weismann, amongst others. By the germinal theory of inheritance I mean the view, already stated above, that the characteristics of organisms are determined by the potentialities existing in the germ-cells which give rise to them; and are not determined, as they are

according to the theory of ancestral contributions by the somatic characters of their parents and ancestors. And I submit that the words of Weldon's which I have quoted, show that a belief in the latter theory has persisted at least as late as 1901, and that there is therefore some justification for the view that what I have called the third period begins, roughly, with the 20th century.

I cannot better recall your attention to the tentativeness of this brief outline than by quoting part of the conclusion to the Zoonomia. "What I have thus delivered I beg to be considered rather as observations and conjecture, than as things explained and demonstrated."

LECTURE II.

THE ATTEMPT TO TACKLE THE PROBLEM OF INHERITANCE BY STUDYING THE PHENOMENA OF CROSS-BREEDING.

THE MENDELIAN PHENOMENON.

IN the summer of 1820, the year in which Mendel was born, John Goss, living at Hatherleigh, a village some eight miles due north of the northern boundary of Dartmoor, crossed a yellow-cotyledoned[1] variety of the culinary Pea with a green-cotyledoned variety of it, and found that the hybrid thus obtained was yellow-cotyledoned, or, as we may call it for short, " yellow." He found that these yellow hybrids gave rise in the next generation to both yellows and greens; and further that, whilst all these yellows, as he thought, gave rise to yellows and greens again, the greens all bred perfectly true. Those who are familiar with the Mendelian phenomenon will recognize that Goss witnessed the phenomena of Dominance and Segregation and also the fact of extracted recessives (the greens) in F_2 breeding true.

I will allow Goss to describe his results in his own words[2]:
" . . . . . I have raised some new varieties of peas, and as one of these appears to be at least a singular production, and finding very little on this subject in your volumes, I am tempted to give you a description of it accompanied with a few observations.

In the summer of 1820, I deprived some blossoms of the *Prolific* Blue of their stamina, and the next day applied the pollen of a *Dwarf Pea*, and of which impregnation I obtained three pods of seeds. In the following spring when these were opened in order to

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[1] By a yellow-cotyledoned Pea I mean a Pea-plant whose first two leaves or cotyledons are yellow. Similarly with a green-cotyledoned Pea. I shall revert to this question later.

[2] Horticultural Transactions, Vol. V., p. 234.

sow the seed I found to my great surprise, that the colour of the Peas instead of being a deep *blue*, like their female parent, was of a *yellowish white* like the male. Towards the end of the summer I was equally surprised to find that these white seeds had produced some pods with all blue, some with all white, and many with both blue and white peas in the same pod.

Last spring I separated all the blue peas from the white and sowed each colour in separate rows, and I now find that the blue produce only blue, while the white seeds yield some pods with all white and some with both blue and white Peas intermixed.

The edible qualities of this Pea I have not tried, having but few . . . . . ."

Later on he says "should this new variety of Pea neither possess superior merit, nor be deemed singular in its bi-coloured produce, yet there is, I conceive, something in its history that will emit a ray of physiological light . . . . . ." Little can Goss have imagined how fully that prophecy was destined to be fulfilled eighty years later.

The phenomena as they appeared to Goss may be summarized in the following diagram, in which Y signifies yellow and G, green.

$$Y \times G$$

$$Y \qquad F_1 \text{ generation.}$$

$$Y \qquad G \qquad F_2 \text{ generation.}$$

$$Y \qquad G \qquad G \qquad F_3 \text{ generation.}$$
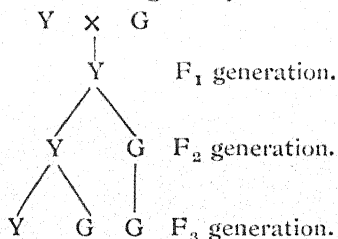
Those who are familiar with the details of the Mendelian phenomenon will see that this is a correct account of what occurs, except that Goss imagined all the yellows in F_2 to produce yellows and greens, and that he does not give the relative number of yellows and greens in F_2.

Let us see what actually occurs. In the first place the ratio of yellows to greens in F_2 is as 3 to 1. With regard to the other point, let us reflect for a moment what a consideration of the ancestry of the F_2 generation might lead us to expect[1]. If we look at the ancestry of the F_2 generation we find only one type of green ;

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[1] This looks as if we were looking to the ancestry to give an indication of what will happen in F_2. This is indeed the case. But it is to be noted that the difference between the ancestors to which we pay attention are not somatic ones but relate to the nature of the offspring (whether uniform or diverse) of the several forms.

the stable, pure-breeding, type with which the cross was made, and we might expect that when the green reappears it will breed true : and we find that it does. But when we look at the yellows in the ancestry of F_2, we find that there are two types, the pure-breeding stable type with which the cross was made, and the unstable type, which produces both yellows and greens, which composes F_1. So that we have three possibilities before us with regard to the yellows in F_2 ; they may be all stable or pure-breeding, they may be all unstable or hybrid, or some of them may be stable and some unstable. Mendel found that the last case obtained; and, moreover, determined the proportion in which the two types occurred amongst the yellows; he found that amongst every three yellows in F_2 two were, on the average, unstable and one was stable. He also found that the composition of the generation produced by F_2 Hybrid Yellows was the same as that produced by the F_1 Hybrids.

So that we are now in a position to exhibit the Mendelian phenomenon in the following diagram.

$$Y \quad \times \quad G$$

(Hybr.) Y F_1

1 (pure) Y   2 (Hybr.) Y   1 G F_2

(pure) Y only   1 (pure) Y   2 (Hybr.) Y   1 G   G only F_3
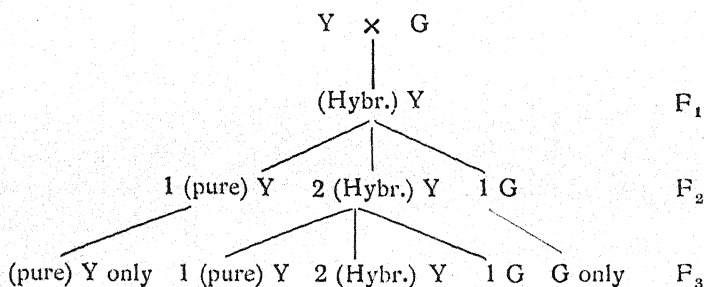
Before we proceed with our argument it may be interesting to pause for a moment and see how it was that Goss missed what Mendel saw. The cause is not far to seek. Goss was not interested in the interpretation of the phenomena before him. The first sentence after the narration of his results is " The edible qualities of this Pea I have not tried, having but few." To see the phenomenon as displayed in the last figure it would have been necessary for him to record the peas on (*i.e.*, the cotyledon characters of the offspring of) each plant separately. He does not say he did this ; and, from the fact that when he made a separation of this kind, as in the sowing of the yellows and greens in F_2, he expressly refers to it, we may suppose that if he had recorded them separately he would have said so. Besides there is no reason, which we can imagine, why he should do so. He probably left the plants in the ground until they were dry, and picked a few pods from each row at random.

Let us now return to the Mendelian phenomenon. And let me here refer to a simple fact which, by reason of its very simplicity, is in danger of being overlooked, unless especial emphasis is laid on it at the outset. It is the fact that Mendel did two entirely distinct things; he observed and recorded the phenomenon which bears his name, and he put forward a hypothesis to account for it; I do not suggest of course that this fact is not perfectly patent to those to whom the spread of Mendelian theory has been due. I merely point out that in the majority of available expositions of this theory great stress is not laid on the precise point (which may not be so evident to the reader as, perhaps, at first sight it w uld seem that it should be) at which narration of phenomena ends and statement of hypothesis begins. One result produced by this on the mind of the student is that he inevitably receives the impression that there is as little doubt about the hypothesis as about the phenomena. The phenomena and the hypothesis become so intimately associated in the mind that the idea that the one stands or falls with the other, takes root. The result is that the upholders of the theory unconsciously come to regard it as as firmly established as the phenomena, whilst its critics are led, by their scepticism with regard to the hypothesis, to doubt the reality of the phenomena. A fact which has probably contributed largely to this close association in the mind between the hypothesis and the phenomena is that both of them can be and are represented by a singularly diagrammatic and simple scheme. But the two things are perfectly distinct; there is no question about the simple facts which I have narrated so far: I shall give the details of the evidence on which the statements as to the Mendelian phenomena presented by crossing yellow with green peas are based shortly. But although evidence favourable to the theory is being rapidly accumulated we should be rash indeed, in my opinion, if we were to regard the truth of the hypothesis as finally established. Another cause contributing to the association between these two things which it seems to me so important to keep apart, is that both take shelter under the one word Mendelism.

I shall endeavour to emphasize the importance of keeping the two in separate compartments in the mind by not stating the hypothesis until the next Lecture and by not using the word Mendelism again.

Let us now proceed to the consideration of the evidence for the phenomena which I have so far related. And in doing so I propose to confine myself to the evidence for the statement that, in

each generation bred from the hybrids, recessives occur in the proportion of 25% of the whole of the generation.

I have taken the Tables printed below from Mr. Lock's valuable paper on "The Recent State of Knowledge of Heredity in *Pisum*,"[1] and incorporated my own published observations[2] on this point.

Generation.	Observer.	No. of Yellows.	No. of Greens.	% of Greens.
F_2	Mendel ...	6022	2001	24·9
	Correns ...	1394	453	24·5
	Tschermak	3580	1190	24·9
	Bateson ...	11903	3903	24·7
	Hurst ...	1310	445	25·4
	Lock ...	1438	514	26·2
	Darbishire	4015	1394	25·8
F_3	Correns ...	1012	344	25·5
	Tschermak	3000	959	24·2
	Lock ...	3082	1008	24·6
F_4	Correns ...	225	70	23·7
	Lock ...	2400	850	26·1

Mendel continued the experiment with cotyledon colour through six generations, but on a small scale, and he does not give any further information than that "no departure from the rule has been perceptible." It is to be supposed that he recorded the numbers of yellows and greens, but did not think them of sufficient interest to warrant their publication. I shall have occasion to revert to this highly important fact later.

For the present I am only concerned to point out that all the evidence we possess as to the proportions in which the recessive member of the pair of characters we are at present dealing with occurs, is contained in the Table given above. Now the expectation based on Mendel's theory is that hybrids will continue to produce recessives in these proportions to infinity. But so closely have Mendelian fact and hypothesis become associated that some of those

[1] Ann. R. Bot. Gard. Peradeniya, IV., 1908, p. 93.
[2] Proc. Roy. Soc. B., Vol. 81, p. 70 and p. 78.

who have given expositions of Mendelian doctrine do not clearly distinguish between what, on the theory, we expect will happen and what actually does. One author for instance, referring to the production of recessives in definite proportions says that the hybrids " will repeat the process and proportions practically for ever."

Let us now examine the Mendelian phenomenon displayed in the diagram on p. 172 in the light of the theory of ancestral contributions. Two of the things which happen are contrary to the expectation based on that theory; one is the unexpected breeding true of all the greens and one-third of the yellows which appear in F_2 : the fact, however, that the offspring of these forms continue to breed true in subsequent generations becomes more in accordance with expectation based on the ancestral theory as we proceed away from F_1. On the other hand whilst the production, by the remaining two-thirds of the yellows, of yellows and greens in the ratio $3:1$, does not give cause for much surprise when it occurs in F_2, the fact that these hybrid yellows continue to do so for six generations becomes *more* remarkable (*i.e.*, less in accordance with the contributional theory) in each successive generation as we proceed further from F_1.

It is seen therefore that the Mendelian phenomenon itself strongly negatives any theory of inheritance according to which the characters of a given generation are determined by the somatic character of its parents and, in a diminishing degree, of its ancestors. That these somatic characters play no part at all in determining the characters of progeny is an entirely novel conception, the acceptance of which is due in large part, as I have suggested, to the combined weight of the work done by Weismann and Mendel.

I think it will be desirable therefore to place before you the result of an experiment[1] which proves in regard to the pair of characters (yellow and green) before us, that the somatic characters of parents and ancestors play no part in determining the nature of their offspring.

The precise point which the following experiment was designed to test was whether the ancestry of the recessive parent of the cross could have any effect on the result of the cross. The recessive parent of the cross was chosen because (in virtue of the fact that two yellows may produce greens, whilst two greens never produce yellows) it is possible to adulterate the ancestry of the green parent with the yellow character to a much greater extent than it is possible

[1] An Experimental Estimation of the Theory of Ancestral Contributions in Heredity. Proc. Roy. Soc. B., Vol. 81, 1909, p. 61.

to adulterate that of the yellow with green; and in this way it was possible to make the difference between the expectation based on Mendel's theory and the theory of ancestral contribution very great.

The green which I used to make the cross with was an "extracted" green in F_5 produced from a cross originally made by Mr. C. C. Hurst who very kindly gave me a sample of F_3 cotyledons. These greens, it will be seen, number no greens amongst their ancestors until the original green used by Mr. Hurst to make the cross, is reached. That is to say its pedigree, if we pay attention solely to individuals in the direct line of ascent and signify yellow by Y and green by G, is as given below, writing only one of each letter where the two parents are the same.

$$\bigcirc\text{Y} \quad \bigcirc\text{G}$$
$$\bigcirc\ \text{Y} \ (F_1)$$
$$\bigcirc\ \text{Y} \ (F_2)$$
$$\bigcirc\ \text{Y} \ (F_3)$$
$$\bigcirc\ \text{Y} \ (F_4)$$
$$\bigcirc\ \text{G} \ (F_5)$$
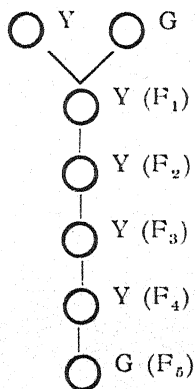
The extracted green used in the experiment is denoted by the circle at the base of the chain. Those familiar with Mendelian theory will see that such a green is, in spite of its ancestry, exactly similar in constitution with a green of pure race, that is a green with nothing but green ancestry for many generations back; whereas, of course, the view based on the theory of ancestral contributions is that it is a very different thing from a green of pure race. And whilst the Mendelian theory would assert that the F_2 resulting from a cross between a yellow and such an "adulterated" green would not differ from the F_2 from a cross between a yellow and green, both of pure race; the theory of ancestral contribution is committed to the prediction that the number of greens in the F_2 from the cross between the yellow and the green with yellow ancestry, will be considerably less than the number of them in the F_2 from the cross between the yellow and green, both of pure race. The difference between the ancestry of the two crosses may be conveniently summarized in the two pedigrees A and B.
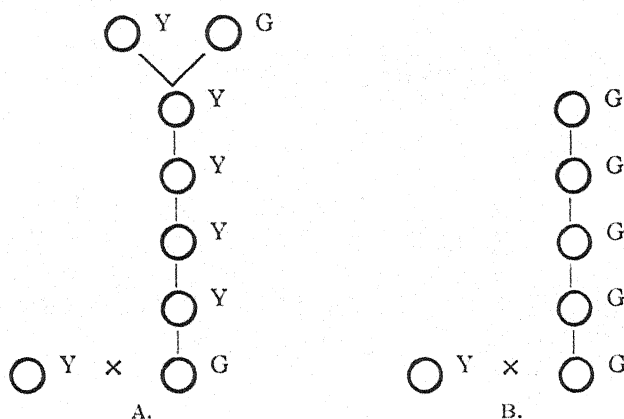
A.	B.
Cross between yellow and extracted green in F_5.	Cross between yellow and green, both of pure race.

Our interest centres in the possible difference between the two F_2 generations produced by crosses A and B. For we know, or expect, yellow to be dominant over green in a cross of type B; *a fortiori*, on the contributional view should we expect Y to dominate over the G used in Cross A.

The Mendelian expectation is that the proportions of yellows and greens will be the same in the two crosses. The expectation based on the theory of ancestral contributions is that the great weight of yellow ancestry, as it may be expressed, behind the green in cross A will diminish the relative number of greens in the F_2 from that cross.

The result of the experiment[1] is entirely in accord with the Mendelian expectation, which proves that the Mendelian interpretation *may* be the correct one, but that the contributional explanation is incorrect. The actual numbers obtained in this F_2 were 105,045 yellows and 34,792 greens, which gives a ratio of 75·12% yellows and 24·88% greens.

All that the experiment just described proves is that the somatic characters of the ancestors behind the parental generation are not effective in determining the proportions of the yellows and greens in the F_2 generation in question; it does not prove, though it strongly suggests, that the characters of the actual forms crossed play no such part. The experiment is incomplete, inasmuch as both are crosses between yellows and greens—the difference between the two crosses lying only in their ancestry. In my next Lecture I shall describe an experiment which proves the correctness

of the corollary, which follows from the demonstration that the character of offspring are not determined by their remoter ancestors, that the somatic characters of the parents themselves play no part in determining the character of their progeny.

Let us return to the fact that Mendel did not publish the proportions in which greens segregated out, in any generation below F_2. Taken in conjunction with the fundamental difference between Mendel's and Nägeli's points of view, this fact is of deep interest. It simply shows that Mendel had no preconceived ideas with regard to that which strikes those of us who have not been fed on Mendelian pap from our intellectual youth up, as the most remarkable thing about what follows from the Mendelian theory (and does actually occur for six generations), namely, the phenomenon of the production by the hybrids (bearing the dominant character) in every generation, of individuals bearing the recessive character, in proportions *which do not diminish as we proceed further from the original cross.* It does not strike me as a very wonderful thing that an F_1 Hybrid should produce 25% greens, but it does strike me as a wonderful thing that an F_{10} Hybrid will do precisely the same thing. Yet it is just those generations about which we who are just freeing ourselves from a belief in ancestral contributions are most anxious to know, about which Mendel gives us least information. This would certainly seem to indicate that Mendel approached his subject unprejudiced by the theory of ancestral contribution in any form. And if this is true it helps to explain how it was that Mendel came to attack the problem in the right quarter by directing his attention exclusively to the contents of the germ-cells, and incidentally how it was that Nägeli entirely failed to appreciate Mendel's point of view.

Nevertheless, although I have grown out of expecting the proportions in which recessives will be produced by hybrids are bound sooner or later, in the course of generations, to diminish, I feel that it is very important to dwell on the distinction between being certain on *a priori* grounds that the proportion of recessives in F_{10} hybrid families will be the same as in F_2, and *a posteriori* knowledge that this is the case. The F_8 generation from the cross made by Mr. Hurst in 1902 I hope to record this autumn—the plants are in flower now—so that I hope to be able to place on record the composition of generations F_2 to F_{10} inclusive, during the winter of 1911.

I have laid this stress on the manner in which the Mendelian

phenomenon itself stands in such sharp contrast to what our pre-conceived ideas about the relation between successive generations would lead us to expect, in order to support my thesis that the new ideas introduced by the study of hybridization are in reality of two distinct kinds : (i.) those new conceptions introduced by both Mendel and Weismann and (ii.) those ideas which are exclusively due to Mendel and his followers.

But I also wish to lay stress on the experiment which I have recorded for another reason. Mr. Lock adds a postscript to his paper on the " Present State of Knowledge of Heredity in *Pisum*" to which I have already referred, which involves a question relating to the interpretation of natural phenomena which is, in my opinion, of first-rate importance. The postscript was as follows :—" In *Nature* of August 22nd, 1907 there appears an anonymous statement to the effect that no one has repeated Mendel's experiments with the deliberate intention of testing the Mendelian interpretation of the results. The curiosity naturally excited by this statement as to what other object—in the opinion of the writer of the review—could have been in the minds of all those who have laboriously continued Mendel's inquiries, is only partly allayed by the explanation of the same writer in *Nature* of September 12th. Here we find that what was meant was that crucial experiments had not been carried out by *sceptical*[1] observers on certain lines which are indicated.

In addition to numerous crosses between heterozygote and recessive carried out with sufficiently conclusive results in the case of peas, the present writer has actually carried out on a considerable scale an experiment with *Zea Mays* on lines closely similar to those indicated in *Nature* of September 12th, 1907. An account of these experiments appeared in *Nature* of October 20th, 1904, and a full description of them has since been published.[2]

I feel bound to add that since the successful issue of these experiments I am no longer sceptical as to the accuracy of Mendel's experiments or of his deductions from them. And if, as it would appear, *Nature's* reviewer demands confirmation by an observer who shall remain sceptical after the event, I am afraid his doubts are unlikely to be done away with. For I know of no sane person who has carried out a reasonable number of experiments on Mendelian lines and still retains the required mental attitude."

[1] Mr. Lock's italics.

[2] R. H. Lock. " Studies in Plant Breeding in the Tropics, III. Experiments with Maize." Ann. Roy. Bot. Gardens Peradeniya III.

I should first like to draw the reader's attention to a remarkable instance of that close association which, as I have said, exists in the minds of some of those engaged in Mendelian enquiry between the Mendelian phenomena and their interpretation. I refer to the first sentence in the last paragraph, which I have italicised. Mr. Lock thinks that because I declared myself (for I was the anonymous reviewer) to be not yet satisfied with the explanation, therefore I cast doubt on the facts to be explained. I do not doubt the facts for a moment. Nor did I say I did.

And secondly I did not demand that the observer should be sceptical *after* the event, but that he should approach the phenomena with an active scepticism of every theory advanced to explain them. I undertook the experiment which I have dealt with in this Lecture in a sceptical spirit and, I am much less (if at all) sceptical of the Mendelian interpretation now that I know the result of it. "What other object (than that of testing the interpretation) can have been in the minds of all those who have laboriously continued Mendel's inquiries" I do not pretend to suggest. But it seems to me that to repeat a man's experiments is not to test the interpretation put upon them, but merely to collect new instances of the phenomenon to be explained. To test the interpretation, the experiment must be repeated in such a way that one or other of two possible theories is forcibly put out of court by the result.

A BIOLOGICAL INVESTIGATION OF THE PERIDINIEÆ
OF SUTTON PARK, WARWICKSHIRE.

By G. S. West, M.A., D.Sc., F.L S.

[Text-Figs. 20—26].

LITTLE is known of the Peridinieæ of the midlands of England, or indeed, of any of the low-lying parts of the country, although those of mountainous areas have been to some extent investigated. I have been engaged since October, 1906, in making a more or less continuous series of observations on the general periodicity and life-histories of the Algæ which occur in that fine stretch of primitive country to the north-east of Birmingham known as Sutton Park. Some of these observations have now proceeded far enough to render publication of certain facts advisable, and the present account of Peridinieæ is sufficient to show that there are probably many interesting freshwater members of this group in the less elevated areas of the British Islands.

The species of *Peridinium* which is generally recorded as common in the ponds and pools of flat countries is *P. tabulatum* (Ehrenb.) Clap. et Lachm., but I have found no trace of this organism in either Warwickshire or Worcestershire.

In all, seven species of the Peridinieæ have been observed in the pools and bogs of Sutton Park. Only one of these—*Glenodinium uliginosum*—is a bog species, occurring among submerged *Sphagnum*, the other six having been found exclusively in the helioplankton of Bracebridge Pool, a sheet of water of rather more than sixteen acres. Three of these, *Peridinium aciculiferum*, *P. anglicum*, and *P. cinctum.* var. *Lemmermanni*, are among the dominating constituents of the plankton of this pool at certain seasons of the year, although I have found no trace of any of them among the weeds at the margins.

I.—Glenodinium uliginosum, Schilling.

Although up to the present unrecorded for the British Islands, this organism is probably more generally distributed in British freshwaters than any other member of the Peridinieæ. It is of very rare occurrence in the waters of pools and lakes, but may often be found in great abundance in bogs and boggy ditches, even up to an altitude of over 2,000 feet.

The active individual has a firm, strong wall, and is generally so packed with a dark black-brown pigment that little can be seen of its internal structure. It swims with the characteristic Peridinian revolving movement, combined with a fairly rapid forward progression. The wall gives only a partial cellulose reaction, and is almost stuctureless, although I have imagined at times I detected a faint indication of a system of component plates.[1]
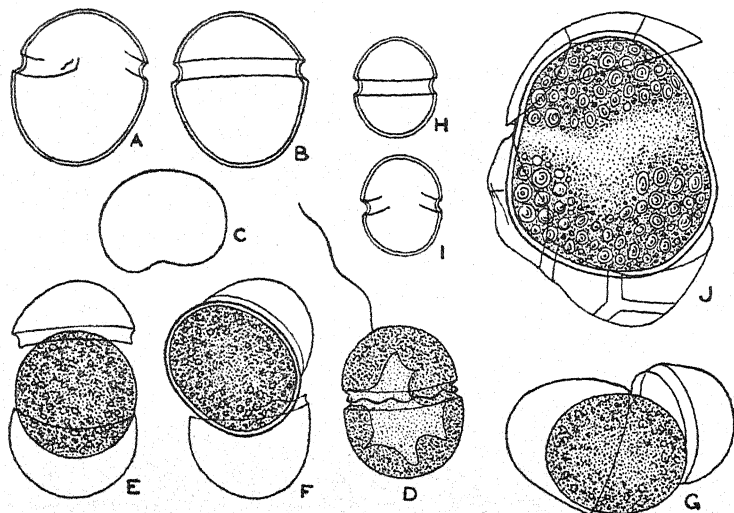
Fig. 20 A—G, *Glenodinium uliginosum*, Schilling. A and B, empty wall showing equatorial groove; C, anterior view showing shallow longitudinal groove; D, young individual developed from a cyst; E, F and G, cyst-formation. H and I, *Glenodinium pulvisculus* (Ehrenb.) Stein. Dorsal and ventral view of empty wall. J, Resting-cyst of *Peridinium cinctum* var *Lemmermanni*. All × 500.

The extent of the equatorial groove is well seen in the empty cell (Fig. 20 A and B), and the less conspicuous longitudinal furrow is fully apparent in a true anterior or posterior view (Fig. 20 C). The evident inequality of the anterior and posterior halves of the cell, the absence of the turgid rims of the equatorial groove, and the complete absence of a red pigment-spot, are characters which appear to clearly mark off this species from *Glenodinium cinctum* (Müll.) Ehrenb.

Glenodinium uliginosum was first noticed in Sutton Park in the autumn of 1906, occurring in large numbers in a boggy ditch among submerged plants of *Sphagnum cymbifolium*, *S. recurvum*, and a long-leaved variety of *Hypnum fluitans*. It occurs in almost all the

[1] Schilling also remarks that in one instance he observed a "Täfelung der Hülle." cf. Schilling, "Die Süsswasser-Peridineen," in Flora, 1891, p. 64.

boggy parts of the Park, among submerged *Sphagnum*, but nowhere in such abundance as in this one ditch. The ditch was easy of access, and I thought it would afford an excellent opportunity for acquiring some information concerning the formation of resting-cysts in this species. Indiscriminate observations in various parts of the British Islands had led me to believe that the formation of cysts in *Glenodinium uliginosum* took place at almost any period of the year, and how far this belief was wrong will be seen from the following observations.

Periodic collections have been made continuously for over two years from precisely the same spot in this boggy ditch, a spot easily marked owing to the proximity of some wooden railings. These collections were commenced in October, 1906, in which month the *Glenodinium* was fairly abundant. Throughout November and December there was a falling off in numbers accompanied by the formation of numerous cysts. Cyst-formation commenced early in November, and by the third week in December the organism had completely encysted. From January (1907) to March, the number of motile individuals gradually increased, reaching a maximum towards the end of the latter month. From the end of March, through April, to the middle of May, there was a reduction in numbers, but from this period there was again a rapid rise to a great maximum in June. In July there was a second minimum, followed again by a third maximum in August. From the middle of August there was a gradual decrease in numbers until by the middle of December the organism had once more completely encysted. The observations were continued through 1908, and show a very similar sequence of three maxima and three minima in the yearly cycle of the organism.

The first maximum is in March, the second in May or June, and the third is during August and the beginning of September. The first minimum occurs in April or May, and the second in July. Only partial encystment occurs, however, and motile individuals can always be found during these first and second minima. The third minimum occurred in the December of three consecutive years, complete encystment taking place, so that for a short period no motile individuals could be found.

The relative abundance of the organism at different seasons of the year has been plotted out on the accompanying chart (Fig. 21), along with a curve of water-temperatures. The temperature of the submerged *Sphagnum* among which the *Glenodinium* occurred, was

carefully registered on every occasion on which collections were made. It will be seen from this comparison that there is a marked relationship between the activity of the organism and the temperature
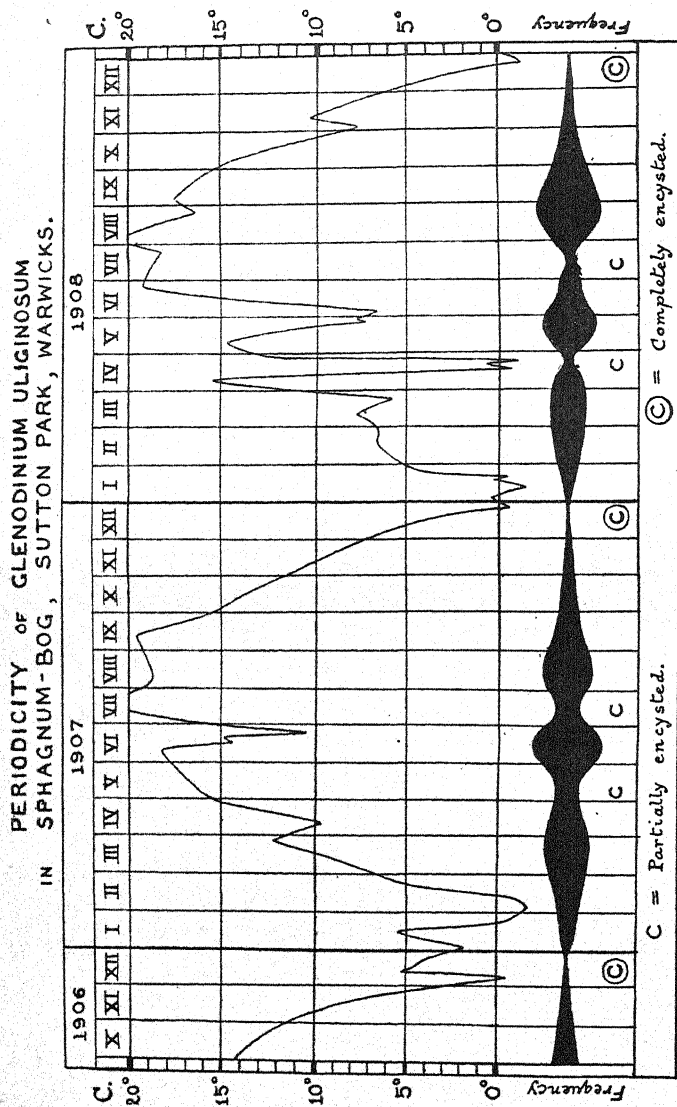
Fig. 21. The upper curve represents the water-temperatures from October, 1906 to December, 1908. The lower black line represents by its varying width the relative abundance of *Glenodinium uliginosum* at different seasons of the year.

of the water. A rapid fall of temperature, especially if prolonged over several months, invariably causes a formation of cysts. The

gradual diminution in the activity of the organism leading to a state of complete encystment in December, coincides with the continuous and prolonged autumnal fall of temperature and the cold period immediately following. The July minimum, accompanied by partial encystment, occurred both in 1907 and 1908 at the period of highest temperature. In 1907 the spring minimum occurred in May, seemingly as a result of a rather rapid rise of temperature, whereas the minimum in April, 1908, was without doubt, due to the cold wintry weather which occurred towards the end of that month.

Thus, *Glenodinium uliginosum*, in the habitat examined, becomes completely encysted for a brief period in December after the autumnal fall of temperature, and much reduced in activity (with partial encystment) in July, at the period of highest water-temperature (18-22°C). Other diminutions in activity, such as those observed in the spring months of 1907 and 1908, may occur either as the result of a sudden cold snap, or of a pronounced rise in the temperature. The organism exhibits its greatest activity when the temperature of the water is between 12° and 17°C, and the optimum temperature lies about 15° or 16°C.

The method of encystment is very simple. The old cell-wall is thrown off in two pieces, which often hang together for some time, and the protoplast rounds itself off (Fig. 20 E—G) The cysts are either globular or broadly ellipsoid, and the newly-formed wall varies much in thickness.

I have not been able to satisfy myself that the chromatophores are small and numerous as described by Schilling.[1] It seems probable that one may get a false impression of numerous chromatophores, owing to the repeated lobulation of a much fewer number of larger ones.[2] Also, it can be frequently observed in the young individual developed from the cyst (Fig. 20 D), that there are only two or three lobed parietal chromatophores.

The dimensions of the Sutton Park specimens were as follows:— length of cell 36-43μ; breadth 34-38μ; max. thickness 26-27μ; diam. of cysts 33-40μ.

II.—GLENODINIUM PULVISCULUS (Ehrenb.) Stein.

This species occurred very sparingly in the plankton of Bracebridge Pool during August, 1908. No cysts were observed. It is

[1] Schilling, l.c., p. 64.
[2] Consult the chloroplasts of *Cosmarium Debaryi*, as figured by Lütkemüller in Oesterr. botan. Zeitschrift, 1893, t.3, f.25.

the smallest species of the genus, the cells having a length of 26—27μ and a breadth of 22μ (Fig. 20, H and I.)   The examples agreed well with both Stein's and Schilling's account of the species, and also with specimens which occurred abundantly in the plankton of Tanganyika and Lake Nyasa.

III.—Peridinium aciculiferum, Lemm.

This interesting species was first described by Lemmermann[1] as occurring near Berlin.   In a later paper on the phytoplankton of the " Muggelsee "[2] he records it as occurring from February to April, with water-temperatures varying from 2·9°C to 12·1°C. Ostenfeld has also found the species in the plankton of Thingval-lavatn in Iceland.[3]   It appears in that lake in January and June, having its maximum from February to March with a water-temperature of 1°C.

In the plankton of Bracebridge Pool, *P. aciculiferum* occurred from February to March in 1907, and also from February to March in 1908.   In each year it attained its maximum in March (with water-temperatures of 5·0°C and 5·1°C) and completely disappeared before the end of the month.   It has thus but a fleeting existence in the plankton, although in March it is one of the dominating constituents.

The occurrence of this species in great abundance in the early spring plankton of a Midland pool is of great interest, as it is essentially a cold-water species, and possibly a northern type. Curiously enough, I have not yet found any trace of it in the spring plankton of the English Lake District, nor in any Welsh or Scottish lake.

P. aciculiferum appears to be well-marked by its three posterior flattened spines.   In the general disposition of its plates it agrees closely with *P. umbonatum* Stein, and this fact has recently induced Lemmermann to place it as var. *aciculiferum* of that species[1].   In the Midland specimens the plates were very indistinct.   They could always be discerned in the empty cell, but were generally too faint for their exact disposition to be ascertained.   The cells are some-what more compressed than in the majority of the species of this genus, and I find considerable variability in the general proportions

[1] Lemmermann in Ber. Deutsch. Bot. Ges., 1900, XVIII., p. 28.
[2] Lemmermann. "Brandenburgische Algen., II.," Zeitschrift für Fischerei, XI., 1903, pp. 86—90, 1909.
[3] cf. Ostenfeld & Wesenburg-Lund in Proc. Roy. Soc., Edin., Vol. XXV., Part XII., 1906, pp. 1126—1128. t. 1, f. 11 20.

of the cell during the great maximum in March. Length of cell 38—48μ; breadth of cell 29—33μ; maximum thickness 22—25μ.

Towards the end of March thick-walled cysts are formed (Fig. 22 C), which undoubtedly sink to the mud at the bottom of the pool, and there rest until the following January or February. These resting-cysts are ellipsoid with somewhat conical poles, and are evidently of the same nature as the thick-walled cysts described by Ostenfeld[2], although not quite of the same form. The extraordinarily rapid disappearance of *P. aciculiferum* about the end of March must be attributed to the simultaneous formation of large numbers of these thick-walled resting-cysts.
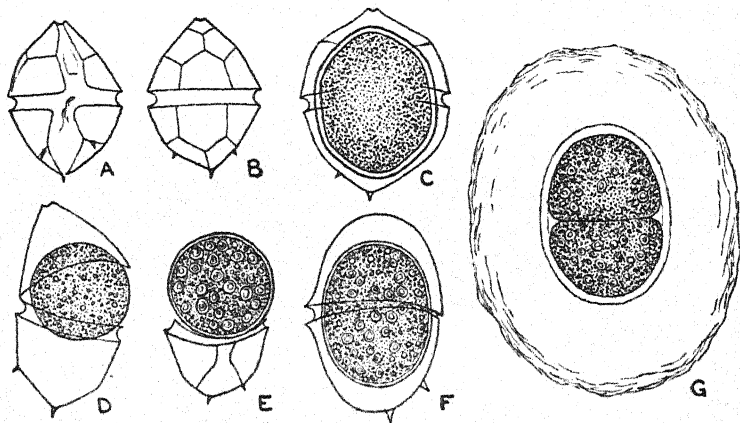
Fig. 22. *Peridinium aciculiferum*, Lemm. A, ventral view; B, dorsal view; C, thick-walled resting-cyst; D—F, thin-walled cysts; G, division of thin-walled cyst. All × 500.

During the time of rapid increase of this organism in January or the early part of February, another type of cyst is formed (Fig. 22 D—F). This is not a resting-cyst, but one which almost immediately escapes from the old cell-wall. It becomes invested by a large gelatinous coat and quickly undergoes division (Fig. 22 G). The two new cells rapidly lose the mucous investment and become typical *Peridinia* with a wall composed of plates.

IV.—Peridinium anglicum, sp. n.

In the plankton of Bracebridge Pool this species attained an enormous maximum in the April of both 1907 and 1908. It made its appearance some two or three months before *P. aciculiferum*,

[1] Lemmermann in Archiv. für Hydrobiol. u. Planktonkunde, IV., 1908, p. 181.

[2] Ostenfeld and Wesenberg-Lund, l.c., p. 1128, t. 1, f. 20.

but although continually on the increase, it did not reach its maximum until a full month after the latter species.

I was quite unable to make the disposition of the plates fit in with any described species of the genus, in consequence of which I sent drawings of it to Mr. Lemmermann of Bremen. He informed me that it appeared to be a new species approaching his *P. Marssonii*[1], and I have given it the name of *P. anglicum*.
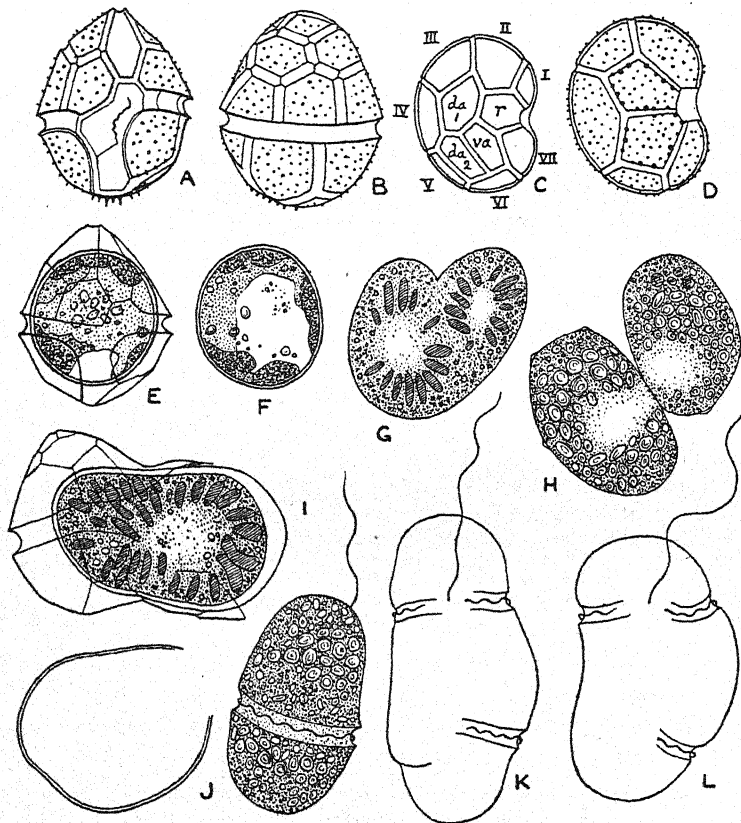
Fig. 23. *Peridinium anglicum*. A, ventral view; B, dorsal view; C, epivalve (anterior half); D, hypovalve (posterior half); E, cyst within old wall; F, escaped cyst; G and H, division of cyst; I, escape of an elongated cyst from old wall; J, escape of motile individual from cyst; K and L, divisions of thin-walled motile state. All ×500.

In Fig. 23 C, I—VII. are the equatorial plates; *r*, the rhomboidal plate; *va*, the ventral anterior (or ventral apical) plate; *da₁* and *da₂*, the dorsal anterior (or dorsal apical) plates.

About the time of its maximum abundance, *P. anglicum* multiplies very rapidly by the production of thin-walled cysts.

[1] Lemmermann in Ber. Deutsch. Botan. Ges. XVIII., 1900, p. 28.

These are globular and formed singly within the adult cell, from which they soon escape by the rupture of the wall in the vicinity of the equatorial groove. Each cyst possesses a large parietal chromatophore with many lobes (Fig. 23 E and F), or two or three such chromatophores. From this stage the multiplication occurs in two ways.

In the majority of observed instances the non-motile cyst divides, each individual then becoming an adult Peridinium and developing a wall of plates (Fig. 23 G and H). This new wall of plates is often evident before the two individuals have completely separated. Sometimes each of the new cells divides again before the formation of the tabulated wall, so that four individuals are produced from the original cyst.

In other instances the cyst gives rise to a motile *Peridinium*-stage with a very thin wall. This at once escapes from the wall of the cyst (Fig. 23 J) and begins to divide while slowly swimming about (Fig. 23 K and L). Several divisions may occur during this motile stage, the resultant individuals each developing a strong wall of plates and becoming a typical adult *P. anglicum*. The flagella are more obvious during this division than at any period in the life-history of the organism, largely owing to the slowness of their movements. All the divisions which take place in the motile stage are in a transverse plane, so that many curious states can be seen in which the body is much elongated and furnished with two transverse grooves (Fig. 23 K and L). The only figures I can find of division of this nature are those given by Penard[1] of what he doubtfully considered as transverse fission in *Gymnodinium viride*.

So far as I can ascertain, this formation of thin-walled non-resting cysts with the resulting rapid multiplication, both in the non-motile and motile states, is a new observation in the life-history of a thick-walled *Peridinium*. It is certainly the reason for the occurrence of prodigious numbers of active individuals of this species in the April plankton of Bracebridge Pool.

The formation of thick-walled cysts was not observed either at the end of April or in May, when this species is rapidly disappearing. Thin-walled cysts continue to be formed up to the time of this rapid disappearance, and it would seem that the last generation of thin-walled cysts persists through the summer and the early autumn as the resting cysts.

The marginal spines bordering the two antapical (or posterior)

[1] Penard in Bull. Soc. Botan. Genève, 1891, t. IV., f. 21 ; t. 5, f. 8.

have all made this error. As the Midland form differs considerably from typical *P. cinctum* in the size and shape of its apical plates, and has retained its features quite constantly for two years, I have named it as a variety.

Diagnosis:—*P. cinctum* var. *Lemmermanni.* Cell. differt a forma typica in tabulis apicalibus epivalvæ multe majoribus et in forma iis typicis non plane congruentibus; etiam tabula equatoria dorsali multe majori. Long. 56—70*μ*; lat. 02—70*μ*; crass. max. 52—53*μ*; diam. 58—68*μ*.

VI.—PERIDINIUM MINIMUM. Schilling.

This minute species occurred only very sparingly in the August and September plankton of Bracebridge Pool in 1908, and most of the specimens seen were dead, empty cells. It has not previously been recorded for the British Islands.

VII.—CERATIUM HIRUNDINELLA. O. F. Müll.

This species, the most ubiquitous and variable of all the freshwater Peridinieæ, is a regular constituent of the summer plankton of Bracebridge Pool. It makes its first appearance in April and gradually increases to a maximum in July or August, after which it rapidly decreases, until by the end of September it has completely vanished. In this pool the maximum is not a large one and the numbers obtained in the tow-nets bear no comparison with the enormous multitudes of *Peridinium anglicum* or *P. cinctum.* It is the first time that this organism has been observed in a British pool of such small dimensions, but its existence as a decided summer form is strictly comparable with its general occurrence throughout Western Europe.

Two distinct forms occur simultaneously, a three-horned and a four-horned form. The latter (Fig. 25 C and D) is a common form in the British lake-plankton[1], and also in the plankton of the lakes of Central Europe,[2] but the former differs in general shape and proportions from any three-horned forms so far recorded from the British Islands. The only published form I have been able to find which approaches this three-horned form from Bracebridge Pool, is

[1] W. & G. S. West in Trans. Roy. Soc. Edin. XLI., Part III., 1905, p. 494, c. Fig. 1 C and D; in Trans. Roy. Irish Akad. XXXIII., Sect. B, Part II., 1906, p. 94, c. Fig. 6.

[2] Consult various papers by Lemmermann, Bachmann, Forti, v. Keissler, Wesenberg-Lund, Brunnthaler, etc., etc.

the one figured by Lemmermann from certain of the lakes of Sweden.[1]

In both 1907 and 1908 *Ceratium hirundinella* formed its characteristic horned resting cysts in September. The increasing size of these cysts during their development causes a dislocation of the cell-wall at the equatorial groove. They apparently rest in the mud at the bottom of the pool from the end of September to the beginning of April.
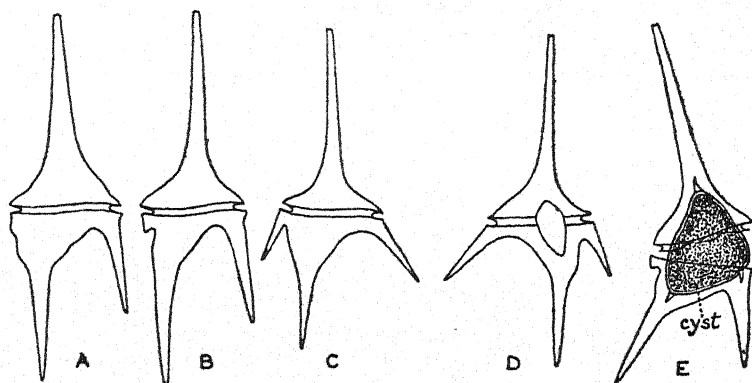
Fig. 25. *Ceratium hirundinella*, O. F. Müll. A and B three-horned form; C and D, four-horned form; E, three-horned form with resting cyst. D is a ventral view; all the other figures are dorsal views. All × 200.

The Periodicity of the Peridinieæ in Bracebridge Pool.

Altogether six species of Peridinieæ were observed in the plankton of this pool, but two of them—*Glenodinium pulvisculus* and *Peridinium minimum*—occurred only in very small numbers in August and September, 1908.

The other four were conspicuous, and three of them dominant constituents of the phytoplankton. The relative frequency of these four species has been plotted out on the accompanying chart (Fig. 26), and it will be noticed that for the years 1907 and 1908 there is a very striking correspondence in the curves. There are two cold-water species and two warm-water species, attaining their maxima in definite sequence each year.

The first one to show activity is *Peridinium anglicum*, which begins in the late autumn, and by January is both numerous and active. Its numbers increase gradually until its great maximum in April. In the meantime, *P. aciculiferum* has appeared, attained a

[1] Lemmermann in Archiv. för Botanik utgifv. af K. Sv. Vet.-Akad. Bd. II., No. 2, 1904, t. 2, f. 48.
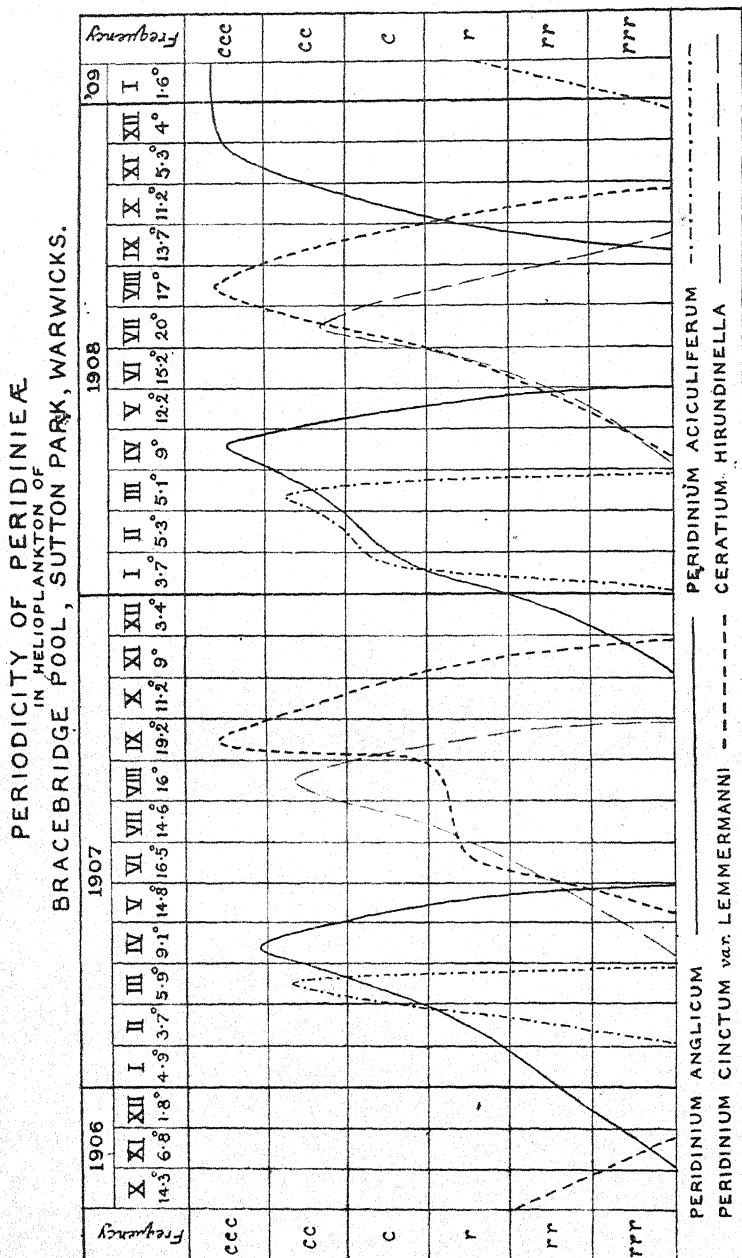
Fig. 26. Chart to show the periodicity of four species of the Peridinieæ, over a period of two years and four months. The temperatures are in degrees Centigrade, and taken six inches below the surface of the water.

great maximum, and disappeared again, all within the short time of two or three months. In 1907 this northern species appeared in February, reached its maximum abundance about the middle of March (temp. 5·9°C), and had completely disappeared before the end of that month. In 1908 it had a similar but slightly longer activity, appearing in January and again attaining its maximum in March (temp. 5·1°C).

P. anglicum very rapidly dimishes after its great maximum in April (temp. about 9°C), and completely disappears by the end of May.

Of the warm-water species, *Ceratium hirundinella* appears first in April, gradually rising to a maximum in July or August (temp. 16—20°C), and quickly disappearing by the end of September.

Peridinium cinctum var. *Lemmermanni* begins its activity in April or May, attains its great maximum in August or September (temp. 17—19°C), and then rapidly and completely disappears by the end of October or November.

It will be noticed from the chart that all four species disappear very rapidly, the curves all having very steep downward slopes. This is to be attributed in every instance to the rapid formation of resting-cysts at the close of the active period. In two species the encysted stage is induced by the vernal rise of temperature, and in the other two species by the autumnal fall of temperature.

Horned cysts were only observed in *Ceratium hirundinella,* and the formation of lunate cysts, with produced and spinate extremities such as those described and figured by Stein[1] in *Peridinium tabulatum* and by Schilling[2] in *Glenodinium cinctum,* was not seen in any species of *Peridinium* in the two years these organisms were under observation.

A curious irregularity is noticeable towards the end of 1908. In this year *Peridinium anglicum* appears to have had a resting period of only a little over three months. It recommenced its activity in September and very rapidly attained a great maximum in November, which it maintained throughout December, 1908, and January and February, 1909. This deviation from the general seasonal periodicity of the organism (as shown during the two previous years) is partly due to the early cold of the autumn of 1908, which was continued right through the winter. At the same

[1] Stein, Der Organismus der Infusionsthiere, Abth. III., Hälfte II., 1883, t. 12, f. 20—28; t. 13, f. 1—5.

[2] Schilling, l.c. t. 2, f. 28—30; t. 3, f. 3—4b.

time, this does not explain the maintenance of an enormous maximum through the cold period ($4°$—$1°C$) when in both the preceding years the greatest maximum was attained at a temperature of approximately $9°C$.

Botanical Laboratory,
Birmingham University.

ON THE CAUSES OF THE ZONING OF BROWN
SEAWEEDS ON THE SEASHORE.

By Sarah M. Baker

(*University College, London*).

[Text-Figs. 27—30].

THE conditions which determine the zonal growth of Algæ between the tidal limits appear likely to be very simple, and thus afford a very promising field for experimental study. The present paper is a contribution in this direction. The actual zonal distribution of Algæ on the shore has been very thoroughly studied by Börgesen,[1] and others. But in order to have a clear understanding of the conditions under which the seaweeds were growing at the particular locality chosen for the present work, a set of measurements was taken to find their vertical distribution in relation to the tides. The experiments were carried out on the eastern side of White Cliff Bay, near Bembridge, Isle of Wight, where there is a continuous stretch of gently inclined limestone and marl rocks upon which the Algæ grow profusely, for a distance of about two miles along the coast.

The level of high water at the spring tide was found by marking from a boat the highest point to which the tide rose on a given rock. This point was used as the standard point of reference. At low tide an observer was stationed at this rock, while two others went down and found the seaweeds. The vertical distance below

[1] Börgesen. Om Alge-vegetationen ved Faeröernes Kyster. Gyldendalske Boghandel, Nordisk Forlag. Kjobenhavn et Kristiania, 1904. Also *Idem*. The Algal Vegetation of the Faroese coasts, with remarks on the phyto-geography. Botany of the Faroes based on Danish investigations. Copenhagen, 1905.

high water was found by sighting across from the reference point to the horizon, and adjusting a slider on a graduated vertical scale into line with this. Sighting to the horizon involves an error of not more than half-an-inch (1.2 cm.) in the more distant readings taken (*i.e.* about 100 yards or metres). By this method the vertical height of any rock could be measured to within an inch or so. Several readings were taken at different points on the rocks for each species of seaweed. The zoning seemed to be similar at all points on the rocks measured. The zones merged into one another, but were on the whole very well defined. The readings were taken as far as possible on gently inclined rocks, and no account was taken of seaweeds growing in rock pools, or even in hollows which might form temporary rock pools, because the seaweeds in the pools were often entirely different from those on the rocks near Thus in a rock pool high up on the shore, in the zone of *Fucus ceranoides*, there were flourishing specimens of *Fucus serratus* and also of *Halidrys siliquosa*, which are usually found below the low water of the neap tides.

The following Table shows the extreme readings, that is those taken on the extreme edges of each zone, and also mean readings taken from the middle of the zones, where each species was at its thickest.

VERTICAL DISTANCES BELOW H. W. S. T.

			Feet.		Metres.
Spring Tide	...	High Water ...	0	=	0
,,	...	Low Water ...	13	=	4·0
Neap Tide	...	High Water ...	3	=	0·9
,,	...	Low Water ...	9	=	2·7

Species of Seaweed.	Upper Limit.	Lower Limit.	Mean Reading.
	ft. ins. mtrs.	ft. ins. mtrs.	ft. ins. mtrs.
Fucus ceranoides - ·	1 9 = 0·5	3 0 = 0·9	2 6 = 0·8
Ascophyllum nodosum	2 3 = 0·7	7 3 = 2·2	3 6 = 1·0 to 4-ft. to 1·2
Fucus vesiculosus - ·	4 9 = 1·4	8 6 = 2·6	5 6 = 1·7
Fucus serratus - ·	5 9 = 1·7	12 0 = 3·7	9 0 = 2·7
Halidrys siliquosa - ·	11 6 = 3·5		
Laminarias - - - ·	12 9 = 3·9		

These readings have been plotted graphically on the diagram (Text-fig. 27). It appears that the time during which the seaweeds
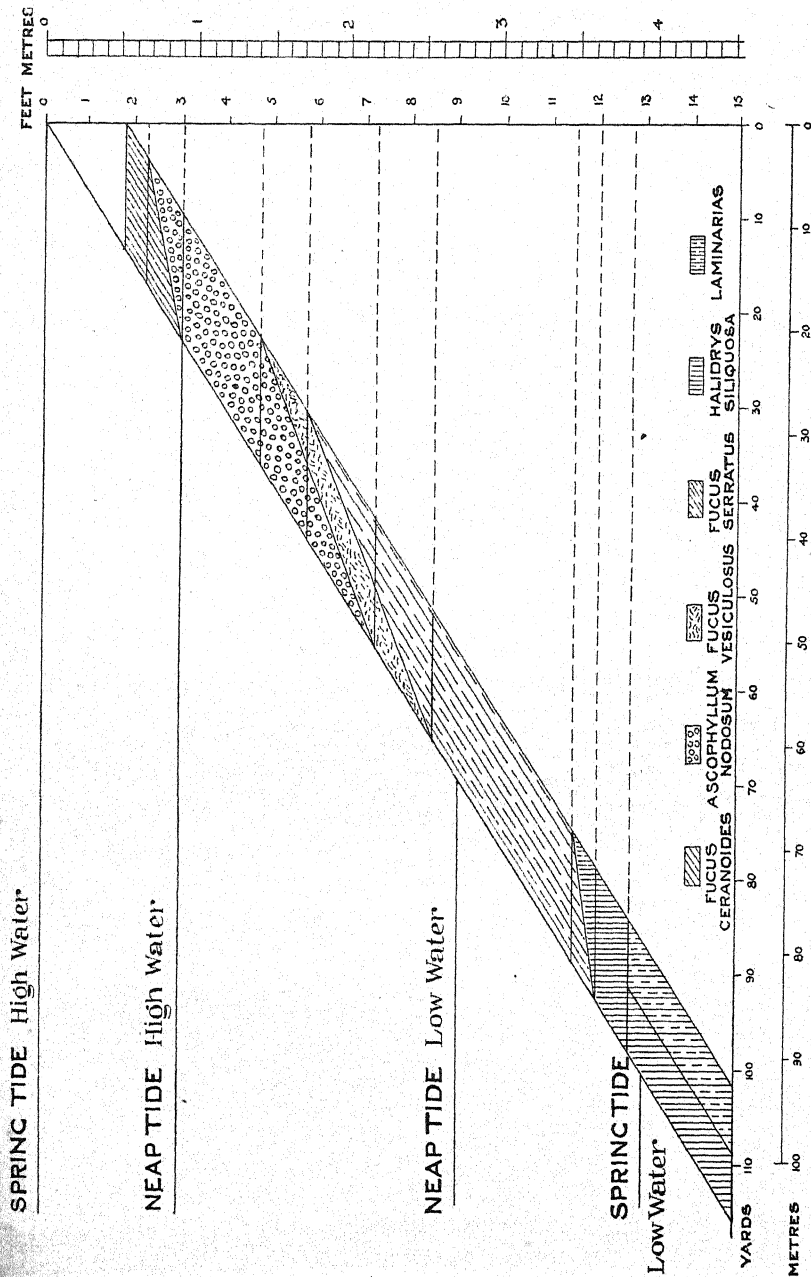
Fig. 27. Diagram representing vertical distribution of Algæ. The horizontal scale is measured at right angles to the line of the shore. The upper side of the diagrammatic section shows the lowest point to which each species descends, while the lower side shows the highest point to which

were covered by the sea was the primary factor in determining the zoning. The rock-pool vegetation confirms this. The seaweeds growing high on the shore were never, or very rarely, found in pools, whereas those which were only uncovered at the lowest tides were found in a great majority of rock-pools.
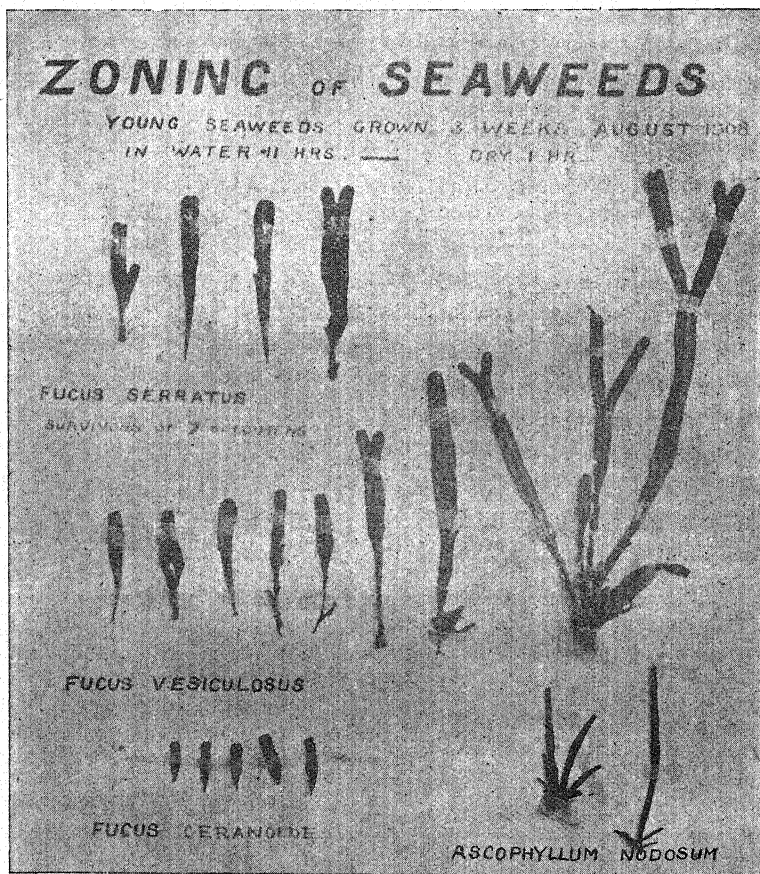
Fig. 28. In water 11 hours; dry 1 hour. × ⅔. *Fucus serratus* grew rapidly at first, but flagged later. *Fucus vesiculosus* grew rapidly; no specimen died. *Ascophyllum nodosum* grew well; no specimen died. *Fucus ceranoides* grew slowly; no specimen died.

There are three phases of the plant's life history which may be influenced by drying, *viz* :—

  1. Germination of the zygote.

  2. Vegetative growth.

mental study, owing to the small size of the gametes. To see whether it would be possible to grow the seaweeds under different conditions with regard to dessication from those to which they were accustomed, a considerable number of very small plants were collected off the rocks, each species being taken from the very centre
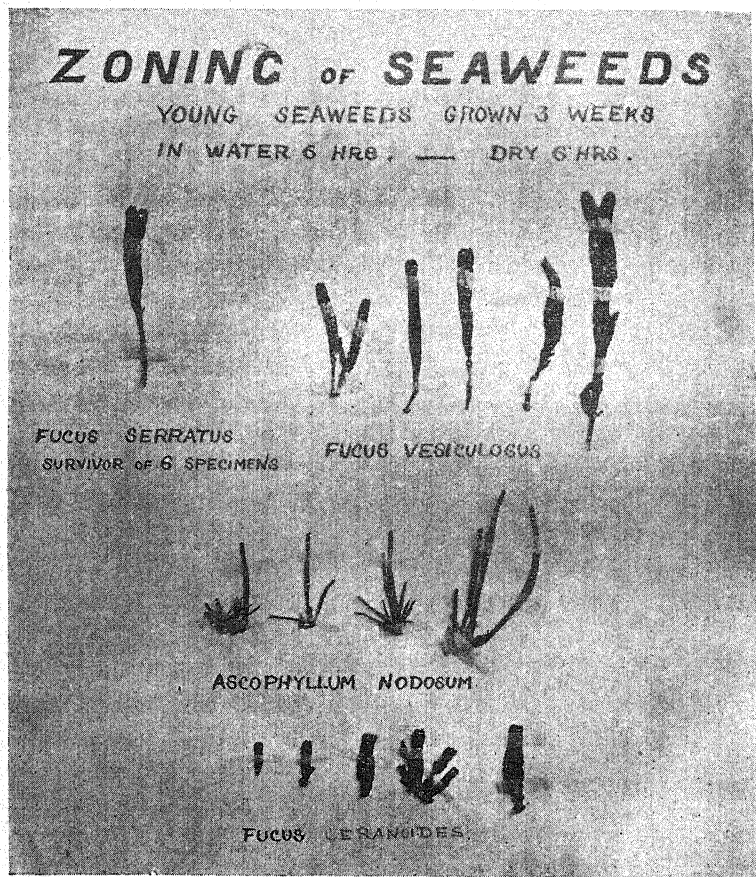
Fig. 29. In water 6 hours; dry 6 hours. × ⅔. *Fucus serratus*; most of the specimens died in about two weeks. *Fucus vesiculosus* grew quickly, but became somewhat shrivelled. *Ascophyllum nodosum* grew well; no specimen died. *Fucus ceranoides* grew best under these conditions.

of its zone; these were divided as equally as possible between three jars. The sea-water in the jars was changed once every twelve hours; but during the course of the twelve hours one jar (A) was left dry for one hour and under water for eleven hours; the second (B) was dry for six hours and under water for six hours; the third (C) was dry for eleven hours and under water for one hour. By

this means a rough imitation of the periodic exposure by the tides was obtained. The plants were treated in this way for twenty-four days, and even in this comparatively short period they showed marked differences according to the conditions. Text-figs. 28—30 show the effects on the growth of the different species.
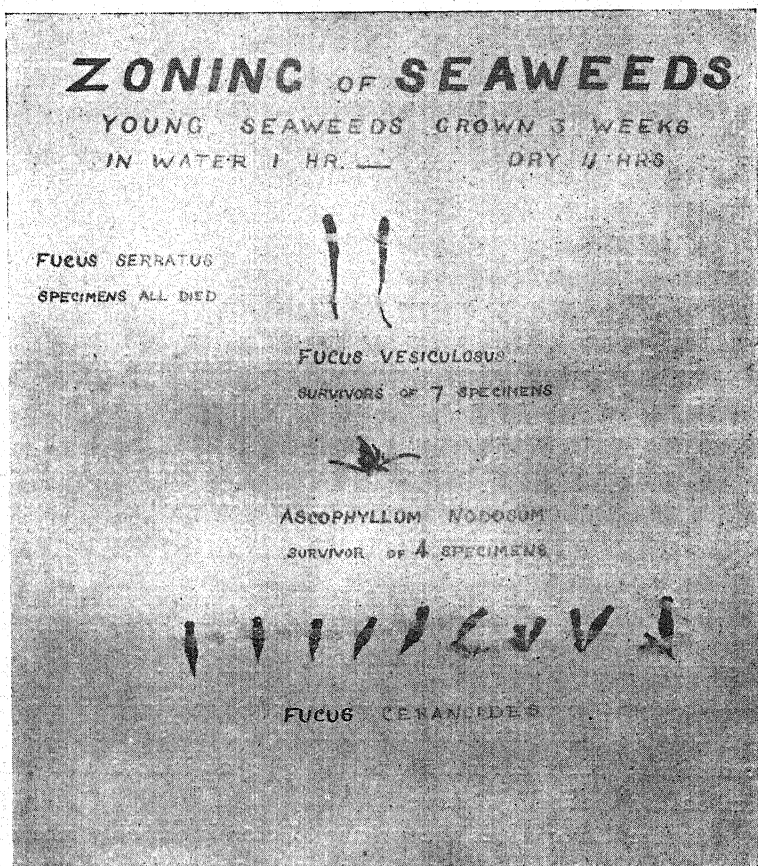
Fig. 30. In water 1 hour; dry 11 hours. × ⅖. *Fucus serratus* died in a few days. *Fucus vesiculosus* grew very little, and became shrivelled at the base. *Ascophyllum nodosum*: growth very stunted. *Fucus ceranoides*; grew slowly; no specimen died.

The specimens of *Fucus serratus* died in two or three days in jar C. In jar B most of the plants flagged in ten to fifteen days, but one was was still alive at the end of the experiment. In jar A they grew very quickly, and after the first six or seven days were far ahead of the other seaweeds in the jar; but after this they

The specimens of *Fucus vesiculosus* grew rapidly in jar A, and none of the plants died. In jar B this seaweed grew quickly, but some of the specimens became rather shrivelled towards the end of the time. In jar C only two specimens just survived, grew very little and shrivelled at the base.

Ascophyllum nodosum grew well in jars A and B, and one specimen survived in C, though much stunted.

Fucus ceranoides was very slow growing in all the jars, but it grew best in B, where there was exposure for half the period. None of the specimens died.

From the way in which the seaweeds grew, one would draw the following conclusions :—

1. That the species of seaweeds growing high up on the shore have a power of resisting dessication, which is not possessed by those growing lower down, and that this power decreases regularly in those species growing towards the lower levels.

2. That the seaweeds which can best resist dessication grow most slowly, and those that grow most quickly are the least tolerant of dessication.

The species which resist dessication most must have most protection from loss of water, and hence will absorb water most slowly; and since these plants get their nourishment from general absorption of water by the thallus, the best protected plants must grow most slowly. In the case of *Fucus ceranoides* there seems to be a definite physiological adaptation against dessication, for it grows best when it is dry for a large proportion of the time. It is probable that, growing on the rocks, the seaweeds would never become so dry as in the glass jars, which were left exposed to all the weather conditions; but the results obtained give an indication of the reasons for the zoning observed.

In the lower zones the primary factor is probably rate of growth; the quickest growing forms would supersede the others. In the upper zones the determining factor is tolerance of dessication. It is easy to see that these factors would cause fairly sharp zoning of the forms with these varying properties. There may be also other factors depending on the reproductive systems of the adult plants on the dispersal of the gametes, and on the power of germination of the zygotes under different conditions.

I have to thank my brothers for kind assistance in carrying out this work.

THE BRITISH VEGETATION COMMITTEE.

SINCE the proceedings of this Committee were last reported (New Phytologist, Vol. VI., 1907, p. 103), five meetings have been held. Manchester, with its central position and other facilities, claimed the winter meetings in November, 1907 and December, 1908; a meeting was held in London in March, 1907, one in Dublin in September, 1908 and one at Cambridge in April, 1909. Attendance is a very good measure of keenness, and it is interesting to note that one-third of the members were present at all five meetings, 80 per cent attended three meetings, while every member has been present at least once. This is an excellent record, when it is remembered that different members live as far apart as London, Dublin and Edinburgh.

It is now nearly five years since the suggestion was first made to combine the scattered forces of the workers on the vegetation of these islands, and the experiment is generally felt to prove its success increasingly with every season that passes. The question of forming a Society with a more extended organisation has been considered more than once, but the smaller body with practically every member actively at work and having a direct vote in all decisions, is still thought by a considerable majority of members of the Committee to remain at present the best instrument for advancing the subject. There are very few serious workers on problems relating to British vegetation, who are not directly or indirectly represented on the Committee, and records are kept of all vegetation surveys in progress in Britain.

EXCURSIONS.

The increasing attendance at excursions, which have been organised on a more elaborate scale than heretofore, is one feature of the period under consideration. A good excursion to the woods and heaths of the Lower Greensand, and to the oak-woods of the Weald in West Kent was made at the end of March, 1907. A small semi-primitive naturally rejuvenating area of oak-wood on Weald Clay was compared with the prevalent "coppice with standards" type. Six members were present on this excursion. A most interesting week[1] was spent on the classic floristic ground of Connemara and Clare, just before the Dublin Meeting of the British Association last year, under the leadership of Mr. Lloyd Praeger,

[1] NEW PHYTOLOGIST, Vol. VII., p. 253.

who circulated an excellent programme several months before, so
that members were able to make the arrangements necessary for
attendance.   There was also a day's excursion over the Wicklow
mountains during the Dublin meeting.   At Cambridge the Committee
business was followed by two days in the open, one in the " Oxlip "
woods on the chalky boulder clay, and the adjoining dry oak woods
on the Lower Greensand, near Gamlingay, to the west of Cambridge,
the other on the heaths near Mildenhall in West Suffolk.   Here
again the local arrangements were carefully made some time
beforehand.   The advantages of such excursions, where leaders
familiar with the vegetation take the stranger to the district over
typical plant-formations, are obvious.

In July, 1908, one of the members of the Committee joined
Professor Schröter's excursion through the Swiss Alps, and a
proposal was then made to arrange an international excursion in
the British Isles.   The idea was heartily welcomed by Professor
Schröter, of Zürich, Professor Flahault, of Montpellier, Dr.
Ostenfeld, of Copenhagen, and other continental plant-geographers.
It is hoped to arrange this excursion in August, 1911, and the
Committee would like, if possible, to extend at least a partial
hospitality to visitors, if funds can be secured for the purpose.

COMMITTEE BUSINESS.

The business at the meetings has mainly centred in one or
two matters relating to standardisation of observations, and the
effect of resolutions adopted may be briefly summarised.

Publication of Maps.   The need for uniformity in scale and
colouring of the published maps relating to " primary surveys "
of vegetation has been felt by the Committee since its formation,
but the publication of memoirs by different Societies has made
such uniformity difficult to secure.   An important experiment in
publication is now being made.   A map of the Peak District of
Derbyshire, comprising two one-inch-to-the-mile sheets (new series),
with a memoir by Dr. C. E. Moss (Cambridge) is now being
prepared for publication, the map being printed at the Ordnance
Survey Office.   It is hoped that this may become a permanent
means of publication, and so remove the hindrances to publication
of primary surveys which have hampered the Committee's work
during the last few years.   In order to maintain a uniform standard
in the memoirs published in this way, the Committee will appoint
annually a " Primary Survey Publication Sub-Committee," whose

business it will be to recommend the various maps and memoirs for publication.

Colour Scheme. After careful consideration, a scheme has been prepared, which can now be obtained (in slip form) from the Secretary (13, George Square, Edinburgh). The basis of this scheme is to give allied types of vegetation related groups of colours, consideration being given to suitable tints and the number of such available. This scheme gives the names of water-colours to represent plant-associations on field-maps, and these are correlated with colours for publication selected from the scheme now in use on colour-printed maps of the Geological Survey (new series). The colour scheme has been prepared by members with the greatest experience over different areas of Britain, and includes all types of vegetation hitherto recognised, while the probability of new colours being required has not been overlooked.

Nomenclature. This difficult subject has been discussed from time to time, and the Committee has decided to make a statement on the subject at the International Congress at Brussels in 1910, where a special effort is to be made to deal with the nomenclature of vegetation. The basis of the statement will be an attempt to determine more closely than has hitherto been done, the conception of a "plant-formation" as the basal conception in descriptive ecological plant geography.

Botanical Photographs. The arrangement already outlined (NEW PHYTOLOGIST, Vol. VI., 1907, p. 104) has been adopted, so that all botanical photographs submitted and accepted will find a place either in the collection of the Botanical Photographs' Committee of the British Association, or in that of this Committee. The former collection is under the control of the Secretary of the British Association Committee (Professor Weiss, Manchester), while our collection is under the charge of Mr. Tansley, at Cambridge. The collections are now fairly large and are available for reference on application.

"Natural Monuments." The recent publication of Dr. Conwentz's book, "The Care of Natural Monuments" (Camb. Univ. Press, 1909), led to a consideration of the Committee's position regarding these. The author indicated that the investigations of members of the Committee were likely to lead to the location of areas of vegetation which it would be desirable to preserve as "natural monuments," and the Committee has now
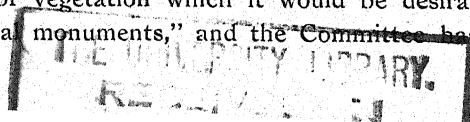
decided to schedule these as they are found. The recent election of a member of the Committee (Professor F. W. Oliver) to the Executive Committee of "The National Trust for the Preservation of Places of Historic Interest and Natural Beauty" will go far to secure the support of that organisation to any efforts which it may be desirable to make to preserve such areas. It appears that the Executive of the National Trust is quite inclined to pay more attention to the preservation of areas which have a scientific as distinct from a historic or picturesque interest; and where, as in most cases, these different interests are present together, it should be possible to do effective work in this direction.

Publications. The issue of primary surveys and maps has lagged during the consideration of arrangements for publication. There is, however, no lack of available material, for the selection of the Peak District of Derbyshire for publication, as stated above, had to be made from four pieces of work, each almost equally ready for publication. During the past two years, members have been responsible for about a dozen papers (half of which appeared in the NEW PHYTOLOGIST) on topics arising from investigations on vegetation. Of these contributions, those of Professor Yapp on Marsh Vegetation (NEW PHYTOLOGIST, Vol. VII., 1908, p. 61 and "Annals of Botany," XXIII., p. 275) may be mentioned as examples of careful work and of the application of exact physiological methods to the study of vegetation.

Communications. These constitute a feature of the winter meetings, and both in 1907 and 1908 there have been quite as many as the available time has permitted. A fair proportion have dealt with the classification of British woodlands, and they indicate that this part of the primary analysis of British vegetation is now approaching a condition of finality. The communications on maritime vegetation also indicate steady progress by several members, while the investigations on plant-remains in peat have also provided a good deal of material.

The British Vegetation Committee may certainly congratulate itself on a continuance of its career of usefulness, while the field that lies open before it in the future is practically unlimited.

May, 1909.   W.G.S.

ALTERNATION OF GENERATIONS AND ONTOGENY,

By V. H. Blackman, Sc.D.

(Professor of Botany at the University of Leeds).

IN the January number of this journal Dr. Lang published a very interesting suggestion concerning the relation of the two generations in the Archegoniatæ, and his views were discussed at the Linnean Society, as reported in the March number of The New Phytologist (p. 104). At that discussion most of the speakers were concerned with the current theories of alternation and their relation to the new views, while little attention was paid to the question of the probability of the theory proposed. The views of one who was not present at the Linnean Society on that occasion, and who finds very great difficulty in accepting Dr. Lang's theory of ontogeny may perhaps be contributed to the discussion in this form.

It is not proposed to deal with the thorny question of the mode of origin of the two generations, but almost solely with the question of the physiological reason for the difference of gametophyte and sporophyte.

In Dr. Lang's view the differences in the two generations (in, for example, homosporous ferns) are the result of external conditions. The egg and spore when formed are conceived to be in a perfectly neutral condition, without any tendency to form either gametophyte or sporophyte. As a result, however, of the difference of conditions in which the two cells start their development—the spore free on damp earth and the egg protected and nourished in the archegonium—the product of the two is very markedly different; one becomes the small prothallus, the other the large differentiated sporophyte.

Such a theory is very simple, and, if it could be accepted, would give a very clear idea of the relations of the two generations. The differences between the two are, however, so great that it is difficult to believe that they are solely the result of differences in the conditions of early development. One would also expect that whatever the origin of the two generations, the cyclic processes of alternation would by now have become impressed, at least in part, on the protoplasmic mechanism of development. Further, a protected and highly nourished condition is clearly not necessary for

development of a complicated body, for we know in many animals and plants that an elaborate body may be built up from a free egg.

Apart from experiment (a question which will be dealt with later) the theory can clearly only be discussed on general considerations, on the grounds of its relative probability as judged by developmental processes generally, and especially by those of other organisms with a complicated life-cycle.

One of the chief arguments urged in favour of this view is in the nature of a dilemma. We are presented with two possibilities: (a), " that the germ-cells are so different that they necessarily give rise to bodies of different structure," (b), that the two germ-cells are alike, but the resultant bodies are different owing to the different conditions of early development. Dr. Lang accepts the second view, but to the writer it seems that the first (with the omission of the word " necessarily)" should be accepted as more probable.

There do not appear to be any serious difficulties in conceiving the egg and spore as different, in believing that one has received from the plant which bore it a tendency to become a sporophyte, the other, a tendency to become a gametophyte. The orderly unfolding of the root, stem, leaf and flower in the development of the ordinary plant is explained mainly by internal factors, such as growth correlation and the influence of one stage upon one another. It would seem then a simple extension of this view to apply it to the whole life-cycle of a given organism however complicated, and to consider the various stages as united together by a *cyclical correlation*, one stage influencing the development of the other. It is quite clear that different types of germ-cells of an organism, because they are freed from connexion with other cells, are not necessarily in the same state; one has only to consider the case of zoospores and gametes.

It can easily be shown that the germ-cells in many forms are just as dependent on their position in the life-cycle for the way they shall develop, as are the cells of the primordium of a leaf on their relation to the general body. A single example will make this clear. If we consider *Puccinia graminis* we have no less than four kinds of germ-cells—teleutospore, sporidia, æcidiospores, uredospores. If all these four be placed on a barberry-leaf in moist air the first will form, not an ordinary germ-tube, but a special promycelium; the other three will form germ tubes, but

only that from the sporidium will penetrate the leaf. Obviously all these germ-cells contain all the determinants of the plant, for each is able to reproduce the whole life-cycle. Their difference in behaviour must be due to their different position in the leaf-cycle, to their having received a different "tendency," so that the pro-mycelial characters are latent in all but the teleutospore, the barberry-leaf-infecting characters latent in all but the sporidia, etc.

That the principle of the relation of one stage in development to another must be extended beyond the simple limits of the development of parts of a single body-form is clearly shown by the metamorphosis of many insects. Here we have two very different body-forms, larva and imago, which may pass from one to another, without any change in external conditions.[1] That the relationship between the two body-types is of very special nature is clear from the fact that in many cases most of the larval structures are broken down during the pupa-state and entirely new ones formed for the imago ; and further one type of body may have organs not possessed by the other.[2] If a change of the type of development can take place, independently of a change in external conditions, in the groups of cells in insects, there would seem to be no difficulty in conceiving it as taking place in single cells, such as the spores and eggs of a fern.

The metamorphosis of insects is, of course, only an extreme case of what is so common in animals, the development of larval stages very unlike the mature form. It is the usual absence of such larval stages in plants which makes the dimorphism of the Archegoniatæ appear so striking.

There is another line of argument which points to the fact that cells of the same organism freed from direct connexion with the somatic cells, may yet develop very differently under very similar or identical surroundings. The microspores and megaspores of *Selaginella*, for example, are both free cells developing under almost identical conditions of protection and nourishment, and yet how different are the results attained by the time they leave the

[1] Everyone who has reared silk-worms knows that they will pass from an egg to caterpillar, pupa and imago (moth) under the fairly constant conditions of an ordinary dwelling room.

[2] Within the single egg-cell of these insects there are the cha-racters of two " specific body-forms," one of which develops after the other similarly, and the egg and cell may carry the characters of gametophyte and sporopyte, one being latent in each,

sporangium.[1]   Again, the spore-mother-cell and the egg in an ordinary homosporous fern are both separate cells, both possessing all the characters of the organism; though technically not both germ-cells, they have physiologically a similar relation to the parent plant. They develop under similar conditions of protection and nourishment, yet their behaviour is very different. The obvious view would seem to be that they have impressed upon them in the process of development different "tendencies," in the spore-mother-cell all characters, except that of tetrad formation, being thereby reduced to latency, just as in the development of the ordinary plant the leaf-cells have all determinants, except the leaf-ones, reduced to latency.

It would seem also that we have direct evidence that the spore and egg are different, for even before the spore leaves the sporangium it has clearly started on a different line of development from that of the egg. While both remain protected and supplied with nourishment, the spore surrounds itself with a thick two-layered wall and stores up a certain amount of reserve material, while the walls of the egg remains thin and no material is stored up. The two cells have clearly become adapted to start life under different environments, and this difference of structure, developed while the cells are under similar conditions, cannot easily be explained unless we assume internal differences[2]. The differences in what are called "morphogenic powers" are only separated in degree from these differences.

[1] It may be claimed against this case that the microspores and megaspores are sexually different, and the sex factor may inhibit the developments of secondary sexual (somatic) characters in the two cases. The difference between the microspores and megaspores, however, is not produced by a reduction-division, for the microspore- and megaspore-mother-cells are already different, as their products show. The megaspore mother-cell has clearly in it latent male characters as in development a "parthenogenetic" egg of an angiosperm will give rise to an ordinary monœcious plant. Clearly then the latency of the male characters has been produced in the ordinary process of development apart from the reduction-division. If latency of certain characters can thus be produced in a cell in the ordinary processes of development, why not latency of gametophytic and sporophytic in the egg and spore?

[2] A further assumption can, of course, be made that such cells as spore-mother cells, young spores and the egg are not physiologically separate from the plant, but that their development is controlled, not by their own internal factors alone, but by special chemical substances secreted by the parent plant. Such an additional hypothesis is elaborate and not very probable, and is not borne out by the behaviour of animals where, in allied groups, the egg may develop similarly, whether enclosed in, or free from, the maternal tissue (vide infra). Also it will not explain the different behaviour of the free germ-cells of *Dictyota*, of the Uredineæ, and of the protozoan life-cycle.

The question of the relation of the two generations in *Dictyota* has now to be considered. This point is of great importance, for it was a comparison between *Dictyota* on the one hand (with its somatically similar generations, and its germ-cells developing under similar conditions), and, on the other hand, such forms as ferns (with their dissimilar generation and germ-cells developing under dissimilar conditions), which appears to have first led to the ... from *Dictyota* we have ...ogenetic theory.

... bearing two different types of reproductive organs. The question naturally arises how is this brought about. Why does the tetraspore always give origin to a plant-bearing sexual organs and the egg give origin to a plant-bearing sporangia, when the two germ-cells appear to develop under identical conditions?

There are two possible views:—

(a). That the germ-cells behave differently because of their chromosome number, haploid and diploid respectively.

(b). That the germ-cells behave differently because of their different position in the life-cycle, *i.e.*, that in their development they have received different tendencies.

The hypothesis that the difference in the mode of reproduction is necessarily associated with cytological differences of chromosome-number is, of course, attractive; but just as the view of the relation of somatic differences and chromosome-... has had to be given up so the evidence is clearly against ... objections to such a view are based on general consideration. The serious a certain amount of definite evidence. It is now generally accepted that the diploid cell of any animal or plant contains a double set of determinants (pangens), and every haploid cell a single set of determinants. In the case of *Dictyota* then, every diploid cell will have a double set of somatic, sexual and tetraspore characters, and every haploid a single set of somatic, sexual and tetraspore characters. On general grounds, therefore, the formation of tetraspore-bearing plants by diploid cells alone is not to be explained by their cytological characters, as even the haploid cells possess the tetraspore determinants.

There is also definite evidence against the necessary connexion of the haploid and diploid character with the type of reproduction. In ferns and mosses, diploid gametophytes can bear eggs and

antherozoids, and diploid (so-called parthenogenetic) eggs are of course known in angiosperms also. In animals, haploid, male individuals which produce normal (haploid) spermatozoa are known in the normal life-history of bees and hornets. Delage also has lately succeeded in rearing to a sexual condition a haploid echinoderm produced from a fertilised non-nucleate egg-fragment. It is true that spores have not yet been produced on a haploid sporophyte, but face of the evidence from animals (that germ-cell arise from diploid can develop from hap... considered an impossibility.[1]

Both general considerations and actual ... that the assumption of the relation of cytolo... two types of reproduction is not warranted associated with difference of chromosome nu... regular succession of the processes of fertili... these two processes are never known to oc... cytological differences[2] though the reprodu... associated with these processes may still be ...

We seem then to be driven to the view ... the germ cells have not similar morphogene... the egg is set free with a tendency impress... latent the determinants relating to ... spore has a tendency which keeps ... latent. In other words *Dictyota* sh... one phase of the life-cycle brings ...

Although there ... position in the life-cycle, and very strong evidence for the same in *Dictyota*, the most striking case would be one in which we had an organism with two somatically distinct generations which start life under similar conditions. Such a case we appear to have among animals in the Foraminifera. These are aquatic Protozoa, mostly marine, many of which exhibit a well-marked dimorphism, which may be so distinctly marked that the two forms have been

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[1] Possibly Yamanouchi's artificiality induced haploid sporophyte of *Nephrodium molle* (Bot. Gaz. XLIV., 1907, p. 145) will be found to produce the required stage.

[2] Reduction in haploid cells is hardly conceivable, but it is possible that the diploid eggs obtained in Bryophyta by E. & E. Marchal (Bull. de l'Acad. Roy. de Belgique. Classe des Sciences, 1907, p. 788) and also those of ferns, might be fertilized, when we should have tetraploid cells (which are said to arise in another way in *Polytrichum*). If such forms could be reared their later behaviour would be of great interest.

described as distinct species. If we take *Polystomella* we find two
forms, the *microspheric* and *megalospheric* living under the same
conditions in sea water. The protoplasm of the *microspheric* form
passes out of the cyst and breaks up into a number of brood-cells,
each of which forms a *megalospheric* form; the *microspheric* is thus
the asexual form. The *megalospheric* form is the sexual one
and produces gametes which fuse and give origin to the *microspheric*
form[1]. We have then an alternation of sexual and asexual genera-
tions similar to that of ferns, but both generations start their life
in a free condition in the water and yet they are somatically distinct.
The explanation of the differences between the generations must
clearly be sought, not in external conditions, but in the obscurities
of the protoplasmic mechanism.

The case of other animals which show complicated life-cycles,
parts of which are lived under very different conditions, appear to
give no support to the hypothesis. In the Protozoa where there is
no *soma* the different behaviour of the different cells must be largely
controlled by internal stimuli related to the position of the cells in
the life-cycle. When a mosquito sucks the blood of a human being
infected with malaria, it may draw into its stomach various stages
of the parasite along with the blood. Young amoebulæ, full-grown
schizonts, rosettes and crescents, all alike may be swallowed but
with different results. Only the crescents are able to resist the
action of the digestive juice and of a device to another; clearly we
have a differentiation among the various free cells which brought forward points.
Only the crescents can develop in the mosquito but of the
cannot develop further in man. Later on another type of cell is
formed, the sporozoite, which cannot develop further in the
mosquito but can in man. If a simple form like the malarial parasite
produce free cells with different tendencies we may expect the
in ferns. To take another example, the liver-fluke, *Distomum*
cum, has a complicated life-cycle in which we have three types
of structures, sporocyst, redia and cercaria. They show
considerable differences but all are built up on a common plan,
though the first develops from an egg in water while the other
start their development within the mother-tissues and inside a
molluscan host. The two latter, however, differ considerably,
though produced under fairly similar conditions. These com-
plicated life-cycles in animals would seem only to be explained by
the fact that *cyclical correlation* plays a very large part.

[1] The *megalospheric* form has been seen in some genera to form
similar *megalospheric* forms, this would appear to correspond

A study then of the relations of the generations in *Dictyota* and the Uredineæ, together with a brief examination of animals, like insects and the Foraminifera, which show two body forms, together with evidence obtained from other organisms which show complicated life-cycles, all point to the conclusion that the morphogenetic stimuli are mainly internal, and that, as in the ontogeny of the single body each stage is determined by the preceding stage, so in the more complicated life-cycle each phase is in the main determined by the preceding phase. It is suggested also that a comparison of the germ-cells of Bryophyta and Pteridophyta supports this view.

Of course it is not contended that external factors do not play any part in ordering the life-cycle.[1] Organisms which pass their life under conditions which differ markedly from time to time must clearly make use of such "orientating stimuli." Since, however, it can be shown that *cyclic correlation* plays so important a part (both where the conditions are constant and inconstant), it would seem that such a theory of the relation of the generations should hold the field in any given case, until there is direct evidence to the contrary, or until we have some clearer general ideas of the way external conditions affect development.

The differences impressed upon the germ-cells are not conceived as unalterably fixed. The germ-cells (and somatic cells) contain all the ~~~ organism and under special circumstances which are normally latent may be brought out. A change of external conditions may in the sporophyte cause an alteration in growth relations so that the leaf-cells, which normally have all but leaf-characters latent, may produce shoots. Similarly a change of conditions from the normal may affect the internal factors and cause an alteration in the life-cycle by bringing out certain characters at unusual phases in the cycle.

It has been urged against the view that the germ-cells are different that it complicates the question of heredity. But it has been shown that in other cases there is a clear difference among the germ-cells, as in the Uredineæ, so that the complication must be accepted. How much more complex than in the Archegoniatæ must be the transmission of characters in the insects with a

[1] The internal factors are naturally related to external factors. There is some evidence, for example, that with the increase of the size of the larva of insects there is partial asphyxiation, and that this want of oxygen plays some part in bringing on the changes which lead to the development of the imago.

complete metamorphosis. It is not necessary to assume that there are two completely separate sets of characters for the prothallus and sporophyte, some characters may be in common, as in insects. A certain similarity beween gametophyte and sporophytic characters gives no support to the ontogentic view. A simlariity is strikingly shown in the two body-forms of insects and of Foraminifera.

It is assumed in the ontogenetic theory under discussion that in the spore which develops on soil certain sporophytic characters do not find the conditions suitable for their development and so never appear. When we pass to a form like *Selaginella* some further hypothesis seems to be required to explain why some or all the sporophytic characters do not appear in the developing micro-spores and megaspores, for the conditions in the sporangium may be considered as fairly similar to those in the archegonium.

There is one further criticism which may be made, and that is the question of the importance of the retained position of the egg. It is suggested "that once the dependent position of the diploid generation was established profound and probably sudden changes might be expected to follow, resulting in the difference in body-form between sporophyte and gametophyte." The reason for this view is not quite clear. The egg-cell does not appear to be in such an extremely sensitive condition, for when Heape transferred the fertilized egg from the uterus of one kind of rabbit to another, development was normal. Furthermore, zoologists do not put forward points special significance to the question whether the egg passes stages of development free, or enclosed in the maternal tissues. They do not necessarily find striking differences in the mature organisms as a result of the difference of environment in the early stages of egg development. In *Zoogonoides viviparus*, for example, we have a form which belongs to the same family as *Distomum hepaticum* (the liver-fluke) already mentioned. The egg of the first-named form develops within the maternal tissue, and yet the pro-duct is very similar to that arising from the free egg of *Distomum*.[1]

The question of experimental work is obviously of importance, but it would appear, unfortunately, that very little is to be hoped for in this direction; for not only will critical experiments be of great technical difficulty, but even if experiments are successful the interpretation of them will be exceedingly difficult. The experiments

[1] I am indebted to Miss Lebour of the University of Leeds for this case.

which naturally suggest themselves are the transference of one germ-cell to the natural place of development of the other. It is hardly conceivable, however, that the poorly-clad egg-cell will be able to withstand the rigorous conditions that suit the well protected spore, even if the experiment could be performed ; and the reverse experiment is hardly possible. Even if the first experiment were successful and the egg developed into a gametophyte, the result could hardly be considered as proving that the egg and spore were in an exactly similar state.

Such a sudden change of conditions might easily alter the st of the cell and so overcome the original tendency,[1] for as alre; pointed out it cannot be considered as irrevocable. We know tl a change of conditions may affect the relation of the organs in t development of an ordinary plant-body. The case may be mention(of the female *Lychnis dioica* which, on the attack of a fungus (Ustilag(develops anthers, the normally latent male characters being brough out.

How difficult of interpretation are experimental results is showr. also by Goebel's observations where under similar conditions he obtained from the primary leaves of ferns,[2] not only prothallia and sporophytes, but also a new combination of determinants resulting in a structure intermediate between a leaf and a prothallium. These observations do not lend any support to the view that the externa! factors are primarily concerned in the production of the two body ᷄oduced under the same conditions, and a ᷄ue also. Such difficulties of interpretation are only t ᷄e expected when it is considered how crude such experiments really are. The whole range of the obscure life-processes of the plant li between the actual result of the alteration of conditions and tht phenomena we observe.

Even if it were shown that the egg and spore are exactly similar, and that different external conditions lead to the appearance of sporophytic and gametophytic characters respectively, the result could bear the interpretation that external conditions serve as orientating stimuli to the plant and so decide the question of which determinants shall develop. The two sets of determinants (with no doubt some in common) might still have been acquired by two separate lines of evolution (as has been suggested for the

[1] Such vague phraseology would seem unavoidable while the cell-factors in development are so complex and imperfectly known. What is clear is that the egg and spore contain all the characters of the organism so that under certain conditions any or all of the characters may be brought out.

[2] Einleitung in die experimentelle Morphologie der Pflanzen, 1908, p. 199.

characters of the larva and imago of insects) and the special reaction to external conditions attained independently. The work of Klebs has made us familiar with external conditions which act as "releasing stimuli," and so bring on the sexual or asexual phase in many Thallophyta; but between the way these stimuli act now and the way they have acted in evolution there is clearly a wide gap which can only be bridged by speculation. In the case of teleutospores the onset of autumn conditions appears to act as a stimulus in relation to the development of these structures, but apart from their influence on natural selection the effect of such condition on the origin of teleutospores is very problematical. Similarly the discovery of the conditions under which the sporophyte and gametophyte now arise will not necessarily throw light on the origin of the differences between the two generations.

One does not wish to be unduly pessimistic but until we have further knowledge of the nature of the internal factors which work in development it would seem probable that the exact nature of the physiological relationship of the two generations will remain as inaccessible to direct proof as is the question of the actual history of the two generations. The latter problem has to be attacked on the grounds of " historical probability based on comparative morphology" (to use the words of Professor Farmer) and it would seem that reliance has also to be mainly placed on the comparative method in dealing with the question raised by Dr. Lang. It is suggested that such evidence as is here brought forward points strongly against the " ontogenetic theory," and is in favour of the alternation being a part of the protoplasmic mechanism.

In conclusion one may draw attention to the close similarity of the problems in relation to the metamorphosis of insects and those concerned in the alternation of generations in Archegoniatæ. Information on the subject of this process has recently been brought together in a very interesting way in a small work by Deegener[1]. We have all degrees of difference between the larva and imago. Some organs are rudimentary in both, some are inherited by the imago from the larva, some are common to the larva and imago but follow a different course of development in each, etc. The larva has practically all the organs present in the imago but many organs present in the larva are absent in the imago; hence the imago is probably phylogenetically older than the larva. The two generations are clearly homologous and there were

[1] P. Deegener. Die Metamorphose der Insekten, s. 56, 1909 (Teubner).

probably two lines of evolution from a more primitive form. If the
larva reproduced itself asexually before forming the imago we
should have a condition of things similar to alternation in plants,
and if the larva and imago, in some cases, were to start life under
different conditions we should have a relation exactly parallel to that
of the Archegoniatæ. It is quite possible that some such history as
this has been that of the origin of Pteridophyta; and in fact it is
the ordinary homologous theory. It is interesting to note that the
more elaborate and phylogenetically later body (larva and sporo-
phyte) is in both cases first produced from the egg, the more
primitive (sexual imago and gametophyte) coming later in the cycle.

REVIEW.

"The Oecology of Plants, an Introduction to the Study of
Plant Communities, by Eug. Warming, assisted by Martin Vahl,
prepared for publication in English by Percy Groom and Isaac
Bayley Balfour." Oxford, at the Clarendon Press, 1909. Pp. XI.
and 422. Price 8s. 6d.

THE first feeling aroused on opening this book is one of regret
that an English edition of Professor Warming's "Plantesam-
fund" was not issued at least ten years ago. In the early nineties
of the last century plant-ecology was but little pursued in this
country and formed practically no part of the University curricula.
The subject was indeed in so rudimentary a condition that available
material scarcely existed for teaching purposes. To show students
a few sections of xerophytes and water-plants was about the most
that could be attempted. Professor Warming's "Plantesamfund,"
rendered available to the majority of English botanists in Knoblauch's
translation, published in 1896 under the title "Œcologische
Pflanzengeographie," was the first general text-book on the study
of vegetation in its relation to environment, and a most excellent
account it was. Systematically arranged, clearly written, and
remarkable for its penetrating and judicious treatment of difficult
and obscure topics, it formed a very admirable guide to this
fascinating subject, as it existed fourteen years ago. Its immediate
translation for the benefit of English students was quite obviously
called for. "The difficulties opposing its production" are somewhat
mysteriously alluded to in the prefatory "note" to the present
volume. Whatever they may have been, we can only regret that
they were not successfully overcome long ago. For the present
work, excellent as it is in many ways, cannot be said to stand in the
same relation to the subject as did the "Plantesamfund" in 1895.
Plant-ecology has developed enormously in the interval, both in

Europe and America, and the publication of Schimper's " Pflanzen-
geographie auf physiologischer Grundlage " in 1898 and of Professor
Clements' " Research Methods in Ecology " in 1905 have marked
great strides in that development.   The subject is no doubt, as
Professor Warming remarks (Preface, p. vi.) still in its infancy, but
it is at least out of its swaddling clothes.   And the task of writing a
general text book of ecology which shall be both comprehensive
and at the same time clear and consistent in treatment, has become,
if not, indeed, impossible, at least far from easy.   The scope of
plant-ecology is enormous, and while particular observations have
multiplied with great rapidity, the development of correlating
principles has hardly kept pace.   The subject, as Clements has
pointed out, has developed very unequally.   There has been much
cultivation of the surface phenomena, and too little penetration to
deeper levels.   Into the causes of this we need not enter here, but
the fact has a considerable bearing on the present work.   The great
feature of the " Œcologische Pflanzengeographie " was the consistent
treatment of plant-communities in relation to the water of the
environment, as seen in their primary classification into mesophytes,
xerophytes and hydrophytes, with halophytes standing apart, though
closely allied to the xerophytes.   This classification was a particularly
happy one for the purpose of developing the subject fifteen years
ago, but it was of course provisional, and in the present work has
given place to a much greater number of classes, in which the old
simple relation to water is largely lost.   At the same time the
inclusion of very numerous descriptions of and allusions to local
plant-communities in different parts of the world, about most of
which we know very little, has led to a considerable loss in the
quality of unity of treatment and " Uebersichtlichkeit " which were
such conspicuous features of the original work.   These drawbacks
were no doubt inevitable in view of the development of the subject
we have noted, unless indeed a new principle or principles of
treatment could have been found.   We already have a finely
illustrated and comprehensive treatment of the vegetation of the
world in Schimper's " Plant Geography," and it is perhaps doubtful
if anything on similar lines will serve, at present, any very useful
educational purpose, though as a book of reference for the professed
student of ecology the present work, with its abundant citation of
the most recent investigations, must be of considerable value.

    The general plan remains the same as in the earlier work.
Following upon the Introduction, which is much longer, and contains
a treatment of " growth-forms," there is a section devoted to the
discussion of ecological factors and their action, and then one on
the communal life of organisms and on plant-communities.   A new
section follows, on the adaptations of aquatic and terrestrial plants,
and on ecological classification; and then the plant formations are
treated under thirteen classes instead of the original four.   Finally,
as in the earlier work, there is a section on the struggle between
plant-communities.   The list of literature extends to thirty-two
pages and contains considerably over a thousand titles, including
many works which are not referred to in the text.

    The more extended treatment of *growth-forms* in the Introduction
is welcome.   A short history of the attempts to classify these is
given, culminating with the author's own discussion published last

year under the title "Om Planterigets Livsformer." "It cannot," says Professor Warming, be "sufficiently insisted that the greatest advance, not only in biology in its wider sense, but also in oecological phyto-geography, will be the oecological interpretation of the various growth-forms: from this ultimate goal we are yet far distant." Professor Warming's system is probably the best at present attainable, but we should have been particularly glad of a full treatment of Raunkiär's important researches, too little known in this country, on the kind of protection afforded to buds and shoot-apices by their position and otherwise. This matter is probably one of the most important of all ecological adaptations in plants subjected, as the great majority are, to recurrent periods unfavourable for growth.

The treatment of ecological factors, such as light, heat, water and the various properties of soil, is careful and judicious throughout, but it demonstrates how extremely little we know about their real effect upon plants. In attempting to answer the question "Are the chemical or the physical characters of soil the more important?" —the author concludes "that in some (few) cases, where the soil is specially rich in a chemical substance, it is the chemical characters of the soil, but in other (far more frequent) cases it is the physical characters that are of greatest import" (p. 70). It is no doubt true that where as in Denmark or the North German plain the soil is 'scarcely possessed of any marked chemical characters,' the water-relation becomes almost the sole determining factor, but it by no means follows that chemical characters may not be decisive when these conditions do not obtain. And there is much evidence that this is frequently the case. But we can say no more till a serious experimental attack has been made upon the question. The problems that the ecologist can present to the modern physiologist or can himself attack by the aid of modern physiological methods are literally innumerable, and though some are extremely complicated or even at present unapproachable, others (and among them this) seem to lie open to attack in a fairly straightforward way.

In the new section on adaptations, matter which in the earlier work figured under the heads of the different types of plant-community is usefully brought together. Most of the section deals with the familiar anatomical adaptations of water plants and xero-phytes; there are also short sections on the amount of lignification found under different conditions, on stunted growth, on cushion- and rosette-plants.

An excellent discussion on the determination of plant-com-munities by soil and climate introduces the author's scheme of classification of the communities.

The thirteen Classes into which Professor Warming divides plant communities are as follows:—

A. Soil very wet:
1. Hydrophytes (water-plants).
2. Helophytes (marsh-plants).

B. Soil physiologically dry.
3. Oxylophytes (on acid soil).
4. Psychrophytes (on cold soil).
5. Halophytes (on saline soil).

C. Soil physically dry.
    6. Lithophytes (on rocks).
    7. Psammophytes (on sand and gravel).
    8. Chersophytes (on waste land).
D. Climate dry.
    9. Eremophytes (desert and steppe).
    10. Psilophytes (savannah).
    11. Sclerophyllous formations (bush and forest).
E. Soil physically or physiologically dry.
    12. Coniferous formations (forest).
F. Soil and climate favour the development of mesophilous
        formations.
    13. Mesophytes.

The only one of these classes the contents of which will not, in a general way, be familiar to ecologists, is the eighth, the Chersophytes. These include communities of xerophytic perennial herbs on particular dry soils, often dominated by grasses, but including many dicotyledons, such as the vegetation of certain " Meadows" on the Alps, in Montenegro, in the " Pontic " region, in Spain and Madeira, and also certain " bushland " in North Europe, Chodat's " Garide," and finally " Fern-heath " dominated by *Pteris aquilina* in the south of England and elsewhere. It is impossible to resist the conviction that this class is a kind of "rubbish-heap," including a number of very various and insufficiently studied plant-communities, many of which, at least, have little in common, except that they do not fit into any of the other classes.

But indeed we must regard the whole classification as quite provisional, though in some respects it is no doubt an advance on previous schemes. The class of Mesophytes is altogether too vague in definition. It has to be characterised in terms of itself, as existing where the " soil and climate favour the development of mesophilous formations," which is something like defining civilization as that which obtains under civilised conditions of existence. As an avowedly vague descriptive term referring to plants existing in a medium relation to water, the word " mesophyte " has its use, but we cannot think it should have a place in a formal scheme of classification. On the whole we still prefer Schimper's terms " hygrophyte " and " tropophyte " in spite of the author's criticism, and admitting that they also do not help us much towards constructing a satisfactory formal classification, Coniferous forest, *i.e.* forest of which the trees belong to a definite systematic group should surely not be co-ordinated with the other classes. Sclero-phyllous scrub, in the Mediterranean region at least, is often merely the remnants of coniferous forest, existing under exactly the same conditions of life, and into which for some reason or another the pines fail to get back when once they have been cleared. Then again " psammophilous " vegetation as limited in this book is surely not always, or even generally, independent of the " ground-water," and if we admit this, why should we exclude meadow and forest which is also developed on sands and gravels where the water-level is high ?

There is no fault to be found with Professor Warming's general attitude towards his own schemes.

and says that "the prevailing vagueness in this grouping is due to the fact *that oecology* is *only in its infancy*." This humble attitude, which should indeed be shared by all ecologists, is specially impressive in a writer with Professor Warming's claims to authority. Nevertheless we may well question whether a formal classification on these lines is really worth while until we know a great deal more about the actual physiological relations of the different communities to their environment.

In the next chapter (XXXV) the sub-division of the ecological classes already dealt with into "various less comprehensive types of communities" is discussed, and here we meet with a consideration of the concepts of "formation" and "association." In his earlier work the author refused to use the term "formation" at all, holding that having been employed in so many different senses by different writers it should be abandoned altogether (Œcologische Pflanzengeographie, 1896, p. 10). This attitude could scarcely be maintained, for the term had taken too firm a hold in ecological literature. The word "formation" is a very expressive one, conveying the idea of a specific kind of vegetation "formed" by the conditions of life, and should undoubtedly continue to be used, as it has been by a long series of writers since the time of Grisebach, for the most fundamental unit of vegetation. We have therefore to enquire: what is this most fundamental unit?

Professor Warming, after pointing out the differences of usage by previous writers, gives the following definitions :—

"A formation may then be defined as a community of species, all belonging to definite growth forms, which have become associated together by definite external (edaphic or climatic) characters of the habitat to which they are adapted. Consequently, so long as the external conditions remain the same, or nearly so, a formation appears with a certain determined uniformity and physiognomy, even in different parts of the world, and even when the constituent species are very different and possibly belong to different genera or families. Therefore :—

A formation is an expression of certain defined conditions of life, and is not concerned with floristic differences" (p. 140).

"An association is a community of *definite floristic composition* within a formation; it is, so to speak, *a floristic species of a formation which is an oecological genus*" (p. 145).

Plausible as these definitions may appear, we do not believe that they will be found to furnish a satisfactory basis for the practical classification of vegetation. The assumption that in defining a formation as "an expression of certain defined conditions of life" we are not concerned with floristic differences, but only with growth forms, is not, we think, a sound one. Species may differ in constitution and economy without showing marked differences in growth form, as for instance the beech and the oak, and if it can be shown that such species dominate communities characterised by different associates, and inhabiting different types of soil (as they do in England), it is quite certain that each community is "an expression of certain defined conditions of life," and is, therefore, in Professor Warming's terminology, not an association (p. 331), but a formation. In general we may well doubt if there is any such thing as a *purely* floristic difference between different communities. If it be contended

that beech and oak may grow equally well on the same soil, and in many parts of Europe form natural mixed or alternating woods, the reply must be that every case must be taken on its own merits. The conditions may lead to such a result in one country and not in another. There may be a deciduous forest-formation dominated by alternative trees under one set of conditions, and separate pure-formations each dominated by a single species under another set. To the objection that this is to lay undue emphasis on minor differences and to obscure the wide relations, it must be replied that it is perfectly possible to bring together similar formations, such as the deciduous forests of cool temperate regions, in a unit which may be called a *type of formation.* It is simply a question of a suitable nomenclature. But it is of the first importance to separate communities which are really "the expression of certain defined conditions of life" whether they be characterised by markedly different growth-forms or not. Taking the the taxonomic analogy, we prefer to consider the *formation* as the *species.* The species, after all, is the fundamental unit in taxonomy, as the formation should be in vegetation.

Of previous discussions on the concept of formation we consider Drude's (Deutschlands Pflanzengeographie, Bd I., pp. 285-289), Schimper's (Pflanzengeographie, p. 175) and Clements' (Research Methods in Ecology, p. 292) as the most illuminating. These authors all lay fundamental stress on the habitat. The *differentiating* factor between adjacent formations may be edaphic or climatic, though as Professor Warming rightly insists, any given formation, *considered by itself,* is determined by a *sum-total* of factors both climatic and edaphic. In general, the different geological formations giving rise to different types of soil most frequently bear different plant-formations (though in the case of a "country" covered with a sheet of glacial débris this differentiating factor may be lost), while in mountainous countries different formations are determined by the differences of climate corresponding with altitudinal zones.

We may, however, well consider whether the concept should not be extended in accordance with Moss's usage (Vegetation of Somerset, pp. 12, 68). On one and the same type of soil and under the same climatic conditions we may find widely different types of plant community, *e.g.*, forest, scrub and heathland, or grassland. These differences are very often no doubt brought about by the action of man in disforesting and pasturing, but it is not certain that this is so in all cases. A definite relation always exists between a given type of forest and the corresponding scrub, heath-land or grassland, and the latter types of vegetation tend, in a general way, and subject to arrest by various causes, to go back to the higher type. The different members of each series exist in a habitat which is fundamentally the same, because it is conditioned by the same climate and underlying rock, though it is modified by the relations of the types of vegetation to the soil. It is a question whether, in accordance with the fundamental importance of the habitat, we ought not to include all the members of such a series in the same *formation,* since they are indissolubly connected, and pass imperceptibly one into another not only in space, but in time. The same idea would hold with regard to the natural development of vegetation on bare soils. All the phases of the natural succession

would be regarded as phases in the development of a formation, whose final stage would be represented by the highest type of vegetation possible for the given soil. Only if the substratum is sufficiently changed, after the development upon it of a closed community, by the activity of that community, to initiate a new developmental series, which destroys the community in occupation and finally gives rise to another, should we speak of the development of a new formation. This phenomenon is particularly seen in development of new land through the stage of marsh. The term "association" would find its place in designating each well-defined community, whether transitional or final.

It would be out of place in a review adequately to develop and illustrate these ideas, but it seems probable that the concept of the formation, resting upon that of the habitat, should be extended in in this direction, rather than in that indicated by Professor Warming. The conceptions in question owe a great deal to Clements' insistence on the importance of succession (though his terminology is different) and are in general harmony with the ideas of Cowles and Nilsson quoted by Professor Warming (p. 147) and of Hult (p. 364). It is said (p. 148) that "it does not seem possible to use development as the fundamental basis of classification of plant-communities: for developmental changes are too dependent upon local conditions; a formation does not develop merely in a single definite direction, but will modify in one direction at one place and in another at another place, according to the prevailing conditions." This is all perfectly true, but it does not in the least invalidate the conception of development or change *within the formation*. Rather do these facts lend support to the notion that the true fundamental unit is the sum-total of the phases of such development and change, *under certain defined general conditions of soil and climate*.

There will of course be differences of opinion as to the limits of certain formations, just exactly as there are as to the limits of certain taxonomic species, but the principle described seems to offer the surest because the most natural basis for the concept.

Our plea is for the concentration of attention on the recognition, description and study of the natural units of vegetation (formations in the sense indicated) in different parts of the world, without at present troubling ourselves overmuch about world-wide synthesis. The time is not nearly ripe for that, unless we content ourselves with the more superficial comparisons. It is possible and useful, of course, to recognise the identity of edaphic conditions determining the occurrence, for instance, of reed-swamp all over the world, or the climatic similarities giving rise to the occurrence of the sclerophyll type in the Mediterranean region, Southern California, Southern Chili, the Cape and parts of Australia. But the effective development of ecology during the next twenty years will be on the lines of the recognition and the intensive study of localised natural units of vegetation.

It would be impossible to review in detail Professor Warming's and Dr. Vahl's treatment of the "systematic" portion of their subject. It must suffice to say that an enormous mass of material is dealt with, drawn from all available sources and arranged under the heads already given. As a work of reference this will

certainly be extremely valuable. Many of the incidental discussions are strikingly characterised by the author's skill in dealing with difficult and obscure problems. This remark also applies, in a high degree, to the concluding section on "The Struggle between Plant-Communities," though in the final chapter on the origin of species Professor Warming still finds it necessary to make the assumption " that plants possess a peculiar inherent force or faculty by the exercise of which *they directly adapt themselves* to new conditions, that is to say, they change in such a manner as to become fitted for *existence in accordance* with their new surroundings." The appeal to a generalized " inherent force or faculty " which enables a plant to react *usefully to itself* whatever the nature of the stimulus really does seem to amount to a frank abandonment of scientific method. Surely it is better to say that we cannot understand adaptation at all, than to resort to the assumption of what amounts to a miraculous "faculty" entirely out of line with physical concepts, if we no longer believe that natural selection is a generally effective cause of the origin of adaptations. To the reviewer it seems that the modern tendency to discredit natural selection arises partly from the increasing evidence that Darwin was wrong in attaching the most importance to small indefinite variations in the origin of species, whereas, in reality, the validity of the theory of natural selection in the broad sense does not rest on the nature of the variations that have given rise to species. But this point does not, of course, touch Professor Warming's position, which has all along rested on a belief in so-called " direct adaptation."

The presentation of the book in English (it is not quite clear from the prefatory note whether the author wrote the text in English, or whether Professor Groom translated it) is very satisfactory; though, in the exceedingly difficult, not to say hopeless task, of finding good English equivalents for various foreign technical or quasi-technical terms, we can scarcely congratulate Professor Balfour and Professor Groom on complete success. To take, for instance, the treatment of " moors." In the first place it is doubtful if we can legitimately use the English word " moor " as an equivalent of the German " Moor," *i.e.,* to include all plant communities on peat. To a modern Englishman, at least, the idea of a " moor " does not include the German " Flachmoor " or " Niedermoor," which is generally called in this country a " fen " or " marsh " (though locally the word " moor " still remain, as in Sedgemoor in Somerset, and in the old names of some of the Cambridgeshire fens). In the " New English Dictionary " the meaning of "moor " as " marsh " is given as obsolete. It is always extremely dangerous to restrict or extend the meanings of common words in order to create technical terms. But even, if we allow this (since there is evidence that the word "moor" originally applied to peaty districts in general) "high-moor" is not good as an equivalent of " Hochmoor." " High-moor " inevitably suggests the notion of a moor which lies high above the sea. " Low-moor " is scarcely better for " Flachmoor."

It may be conceded that " fell-field " is a good *etymological* equivalent of the Danish " Fjeldmark," but the use of the English word " fell " (" hill " or " upland country ") is strictly local, nor has

" field " in modern English retained the wide significance of the Scandinavian " Mark " or the German " Feld." " Felsenflur " (given as the German equivalent of " Fjeldmark ") itself does not seem satisfactory, since " Fels " means specifically " rock," and the proposed English term, besides having a slightly ludicrous effect, only makes the confusion worse confounded.

It would no doubt be very convenient if we could find good equivalents in different languages for well-defined and widely spread types of habitat or of vegetation. But it is in most cases impossible without doing violence to the genius of the different languages. In some cases the foreign word has been directly borrowed, as for instance the French word *maquis*, and this is the natural course when the type of vegetation and the descriptive term are native to their own country. But the close relationship of the Teutonic languages should not blind us to the fact that each has developed on its own account and in its own direction, so as to make it impossible, in most cases, to find true equivalents by compounding simple words taken from the everyday language of the people. We think it may be safely laid down as a principle, that a term *derived from any language* must be indigenous to the country of its birth, such as " fen," " moor," " heath " in English, and its technical use must not depart widely from its common use. Any attempt at compounding must be done with the greatest care so as to avoid ludicrous effects and any straining of the genius of the language. It is much better to borrow a foreign term which is really autochthonous than to fall into these errors. In the future, when different types of plant-community are sufficiently known and analysed to make common appellations essential, recourse will have to be made to Greek or Esperanto!

In general we are afraid that the English terminology of the present work will not be satisfactory to English students of ecology.

The book is not quite free from slight mistakes. To mention a few taken at random, we find on p. 18 " sycomore " which should be " sycamore "; " hylophytes " are called " woody plants," instead of " wood-plants " (p. 135) ; on p. 143, footnote 4, " substitute " should be " substituted "; on p. 146 *Holcus lanatus* appears for *H. mollis*, though the species is correctly cited on pp. 95 and 368. *Aira cæspitosa* is evidently written for *Aira flexuosa* on p. 363. This is particularly unfortunate when we consider the very different ecological characters of the species. Three lines lower down on the same page, the statement that " the beech is incapable of natural regeneration " requires qualification. On p. 394 " C. G. Pethybridge " should be " G. H. Pethybridge "; on p. 403 " J. E. Weiss " should be " F. E. Weiss "; and on p. 408, under " Blekinge " the " 2 " should be " 3." " Physically " appears for " physiologically " on p. 136.

Surely it is not true to say that " Moor-soil (in the sense of peat) is probably always acid " (p. 195). Certain types at least of " low-moor " give a neutral reaction. There are one or two cases in which references to British work should have been included. Thus on p. 200 the statement that " The moor, known as high-moor, Sphagnum moor, sphagnetum, or heather-moor, is mainly formed by *bog-moss* (Sphagnum)," requires qualification. In the British Isles, as may be seen from the papers of Smith, Moss and Rankin, of Lewis, and of Pethybridge and Praeger, " Hochmoor " is

typically not formed by Sphagnum. The brief description of Ash-forest on p. 335 should certainly have been supplemented by a reference to the Ash-forest on limestone described by Moss in his "Geographical Distribution of Vegetation in Somerset." The citation of this paper in the bibliography (p. 392) is not quite accurate.

The addition of the initial "o" to the word "ecology" we cannot but regard as savouring of a curious pedantry. The initial "o" has long been dropped in the English language in the case of the word "economy," and the obvious course seems to be to spell "ecology" on the same model, as is always done in America. It is difficult to know how such an artificial archaism can be defended.

The general "get-up" of the book is good, and it is light in weight, while the price is satisfactorily moderate.

A.G.T.

NOTES ON RECENT LITERATURE.

PROFESSOR STRASBURGER ON GENERAL CYTOLOGICAL PROBLEMS.[1]

AFTER an intermission of eight years a new part of Professor Strasburger's "Histologische Beiträge" now appears. The author explains in his preface that, as editor of the Jahrbücher für wissenschaftliche Botanik, his botanical contributions naturally appeared in that journal; the considerable length, however, of the present work demanded separate publication. As a variety of cytological problems are dealt with which are exciting keen interest at the present time, and as the gist of the author's views is not easily obtainable, owing the absence of "General Conclusions," it would seem useful to give a fairly full account of the author's observations and critical discussions.

The first matter dealt with is the interesting question of the determination of sex in the Bryophyta. The appearance in 1906 of the observation of Blakeslee (who showed that the spores of one and the same sporangium exhibited sexual differences) led Strasburger to the idea that the Liverworts might be suitable objects for the study of the question as to whether sex-segregation takes place at the division of the spore-mother-cells. In *Sphærocarpus terrestris*, which had been studied earlier by Strasburger in connexion with the growth of the cell-wall, we have an admirable object, as the four cells of the tetrad remain united within a common exine and germinate in a readily distinguishable group. Further, the young plants produce their sexual organs so early that these can be recognised in plants only 0·1 mm. in diameter. An examination of material sent from Chartres confirmed Strasburger in his view, but the material was insufficient. Later, however, at the request of the author, Professor Douin examined material of

[1] E. Strasburger. Zeitpunkt der Bestimmung des Geschlechts, Apogamie, Parthenogenesis und Reduktions teilung. Histologische Beiträge, Heft VII., 1909, S.XVI, 120, 3 Tafeln. Fischer, Jena, M. 6·50.

S. terrestris and *S. californicus* growing in their natural habitat near Chartres. An examination of 81 groups of young plants, gave 43 with each two male and two female plants; in 21 other cases the differences from the usual rule were easily explained by the unions of tetrads in pairs, or by the fusion during growth of separate thalli, or by the sterility of some of the thalli. Thus 64 of the 81 groups showed clearly that the separation of sex takes place at the time of spore-formation; in 13 other cases the distribution of sex in the groups could not be made out. Four cases, however, remained outstanding, and clearly departed from the rule. One group showed 5 female and 3 male, another 3 male and 1 female, while in two others there were 3 female and 1 male. The exceptions are clearly so few that the segregation of sex at the meiotic divisions of the spore-mother-cells must be accepted as a general rule in the dioecious Bryophyta.[1]

On the observations on *Sphærocarpus* the author bases an interesting discussion on the nature of sexual differences in plants and the point in the life-history at which the male and female tendencies are separated. It is clear that the sexual tendencies are not always separated by the meiotic division. Some Bryophyta are monœcious and even in dioecious mosses when diploid gameto-phytes are raised from protonema caused to develop from the sporogonium, such gametophytes bear both kinds of sexual organs, as E. and E. Marchal showed. We find a similar condition in many homosporous Pteridophyta; a separation of the sexual tendencies only takes place in the hermaphrodite prothallus before the formation of antheridia and archegonia. In the heterosporous Pteridophyta we have the separation of the sexual tendencies shifted back from the haploid to the diploid generation, to the time of formation of the microspore-mother-cells and megaspore-mother-cells. Here again it is clear there is no analogy with *Sphærocarpus,* for the separation of the sexes takes place earlier than, and inde-pendently of, the meiotic division. The dioecism of the heterosporous diploid generation of the higher plants thus presents itself as a problem distinct from that of *Sphærocarpus.* Correns and Noll both agree on the view, based on hybridizing experiments, that the eggs of the dioecious Phanerogams possess a female tendency. For the male products Correns holds the view that half possess male and half female tendencies. Noll, on the other hand, holds it probable that the male cells all possess a male tendency, but in different degrees, half possessing it strongly, half weakly. In the first case it is dominant over the femaleness of the egg, and a male individual would result on such a fusion; while in a fertilisation brought about by a male cell of the second class, the femaleness is dominant over the weak male tendency and a female individual results. Phylogenetic considerations have led Strasburger to the same conclusions as those reached by Noll. The reduction-division in the microspore-mother-cells can segregate male tendencies of unequal strength, but clearly does not separate maleness and femaleness; that separation has taken place earlier. The difference in strength of the male tendency in microspores and pollen-grains

[1] It is interesting to note that Strasburger now definitely gives his adherence to the term *meiosis* as suitable for international use.

does not affect the development of the male haploid generation, whereas on Correns' hypothesis half the microspores being female should produce female gametophytes[1].

When the close resemblance of the higher plants and the Metazoa is considered, the same conclusion should apply to animals, where usually the diploid as well as the haploid generations are distinct sexually. The reducing division should clearly separate the same characters or tendencies in both higher animals and higher plants. The phylogenetic considerations upon which Strasburger lays stress should clearly be taken into account in framing theories of sex; while experimental results are of the first importance, the conclusions drawn from them should be applicable to such classes as homosporous ferns, heterosporous ferns, and diœcious angiosperms. Strasburger is further of the opinion that the sex-characters will not be found to obey the Mendelian rule of segregation. He bases this view mainly on the facts of parthenogenesis, and the observation that commonly diœcious plants may bear branches with flowers of both kinds, or, under the action of special stimuli, hermaphrodite flowers. It is not, however, at all clear what becomes of the minor dose of maleness which, on this hypothesis of Noll and Strasburger, the females receive. Strasburger accepts the view that the egg-cells all bear femaleness, and relates this to the fact that only one egg-cell results from the tetrad. There seems no reason, however, why the egg should not have an equal chance of carrying either maleness or femaleness. Phylogenetic considerations would appear to lead to something of the nature of Castle's original suggestion, that both sexes are heterozygotes.

The next point dealt with by Strasburger is the question of the apogamous development in *Mercurialis* and *Cannabis* described by Kruger. He was unable to confirm these observations; female plants of the two forms kept in a closed greenhouse failed to set seed. Cytological examination also failed to support the view that these forms develop without fertilisation.

The author next turns to the question of the " false hybrids " of Millardet, which completely resembled the male parent. Millardet's observations were made in 1894, but since then Solms-Laubach has made the cross *Fragaria virginiana* ♀ × *F. elatior* ♂, and found that the resulting offspring resembled almost exactly the ♂ parent; they were, however, completely sterile. As these cases are of particular genetic interest, Strasburger investigated the histology of the pollination-process and found it perfectly normal, with a regular fusion of the two nuclei. The only interpretation appears to be that the whole of the characters of one parent are dominant over those of the other.

The next section of the paper deals with the cytology of *Wikstrœmia indica* which was shown by H. Winkler in 1904 to be apogamous and to have abortive pollen grains. The somatic cells, as seen in the tapetum of the anthers and the nucellus and integuments of the ovules, were of particular interest. The resting nuclei of the tapetal cells showed a variable number of granules, rarely as many as 20; their number was inversely proportional to their size. In division-stages of integuments, etc., chromosomes in numbers as low as 6, 7, 9 and 10 were found, though the normal number is 52, since 26 gemini (pairs) are to be seen in the reducing

[1] It is possible that sex of gametophyte and sex of sporophyte are not quite comparable.

division of the pollen. The chromosomes, like the chromatin granules, showed great variety of size, and, moreover, both granules and chromosomes were sometimes clearly seen to be arranged in pairs, or in groups of larger number. As Strasburger showed earlier in *Galtonia* and *Funkia* the reduction in number in these cases is to be considered as a result of the association of somatic chromosomes. It is clear that such association will have no general physiological or genetic significance so long as these elements appear in their full number at the reduction-division. The actual chromosome number is obviously unimportant, for two closely allied species may have widely different numbers of chromosomes, although the number of pangens (or determinants) carried would seem to be about the same. In the modern view the chromosomes are only segments of a thread bearing the pangens in rows.[1]

These observations of Strasburger are of particular interest at a time when the question of the behaviour of the somatic chromosomes is coming more and more into prominence (cf. the previous number of this journal, p. 149). In relation to the behaviour of the embryo-sac-mother-cell of *Wikstræmia indica*, Strasburger finds that although the first division spindle suggests a meiotic phase, yet there is no synaptic contraction and the number of chromosomes is comparable to that of many somatic nuclei, for it is variable and never reaches the full number. There is clearly no reduction. The second division is absent so that no tetrad, but only two sister-cells, are produced, the lower one of which becomes the embryo-sac bearing the diploid egg.

A comparison with other normal members of the Thymeleaceæ, namely, *Daphne Mezereum*, *D. alpina* and *Gnidia carinata* showed that while all these species have 9 chromosomes in the haploid state, *Wikstræmia indica* has 26. In its comparatively large number of chromosomes this species resembles the apogamous members of the Rosaceæ and Compositæ. The apogamous *Antennaria alpina*, for example, has more than twice as many chromosomes as the normal *A. dioica*. As in some other examples, apogamy in this form is associated with polymorphism, for *W. indica* is a collective species. An examination of the various forms placed under this name in the Berlin herbarium showed that more than two-thirds have well developed pollen. A close study of the species would no doubt show all stages from normal, sexual ones to apogamous.

Strasburger then turns to a short discussion of the reduction-division. He points out that a generally accepted view as to the nature of the prophase of this division is still wanting ; in fact, of

[1] When one considers that in a given species the number of chromosomes, though hereditarily fixed, appears to be purely arbitrary, it is astonishing that the variation is usually within such small limits. It may be suggested that individual variations in number (apart from the temporary linkages described above) would probably tend to prevent cross-pollination by rendering difficult the proper pairing at meiosis, owing to the inequality in number of chromosomes derived from the two parents. It would be interesting to compare the variation in chromosome-number of plants normally self-pollinated or apogamous with those normally cross-pollinated. It has already been pointed out by Strasburger that apogamous forms usually have a relatively large number of chromosomes.

recent years, the divergences have become more pronounced. Unfortunately the exchange of preparations initiated by some animal histologists has done nothing to bridge the gulf between divergent views; different observers draw different conclusions, even from the same preparations. This suggests that in many of these cases the phenomena observed are not really sufficient to enable one to come to an accurate conclusion as to the behaviour of the chromosomes. The two points that are really in dispute are, first, whether a parallel conjugation of chromosomes takes place in the prophase of the reduction-division, and secondly, how this association, if it occurs, is brought about. In the unsatisfactory state of the evidence to be obtained from direct observations Strasburger considers that general considerations ought to be brought to bear to help to elucidate the problem.

If there is no pairing of chromosomes and the "gemini" are merely the result of a longitudinal splitting of an original single thread, the production of the special meiotic apparatus of the tetrad division seems quite superfluous, for that division becomes simply two successive ordinary divisions. Again the two halves of the gemini behave quite differently from the two halves of an ordinary longitudinal chromosome as seen in a somatic division ; in the second case the two halves remain close together and only separate in the metaphase, while the halves of the "gemini" become widely separated often throughout nearly their whole length. Further the close relation, often overlapping, of the two divisions remains incomprehensible if both are merely ordinary divisions. If, also, there is no conjugation of chromosomes it is not at all clear why the number of elements is halved and it is only to be explained by secondary hypotheses; whereas a pairing of the elements gives an immediate explanation of the reduction.

There is also the further question as to how the pairing of chromosomes is brought about, whether by parallel conjugation in the early prophase as Grégoire and Strasburger hold, or by lateral approximation in the late prophase of segments of a double chromosome formed by the union of ordinary chromosomes end to end, as held by Farmer and Moore and by Mottier. Strasburger supports his view on the grounds of the pairing of homologous somatic chromosomes which have been observed in many cases and are especially clear where the chromosomes are unequal in size as in *Galtonia* and *Funkia*. Also on the ground that if the gemini are produced by the folding together of chromosome segments the synapsis stages and the curious stretching out of the chromosomes into long threads in the early stages of prophase remain without satisfactory explanation. The simple pairing of homologous chromosomes requires no such elaborate arrangement, for it is found in the somatic nuclei of the plants just mentioned. Strasburger sees in the lengthening out of the chromosomes a means of separating the pangens and allowing the opposition of homologous pairs in homologous chromosomes.

Strasburger professes his scepticism as to the occurrence in *Polytrichum* of two reductions and a peculiar fertilisation by two spermatazoids, as described recently by two Dutch botanists. He also, though it seems with much less reason, throws doubt upon the double nuclear fusion and double reduction in the Ascomycetes.

He is inclined to accept the view of Claussen that, after all, there is in this group only one nuclear fusion, that in the ascus. This view, however, rests on no sure foundation; even if there were some doubt as to the behaviour of the cœnogametic Ascomycetes there can be no doubt about the presence of both sexual and ascus fusion in forms like *Sphærotheca*, *Erysiphe* and *Phyllactinia*. It is somewhat surprising that the Bonn professor should put forward such a view, for the work of Harper on *Sphærotheca*—which first placed the sexuality of Ascomycetes on a firm footing—was done in his own laboratory.

Strasburger then deals with the question of the fixity of the diploid and haploid chromosome-number. He points out that no case of a phanerogam is known with the haploid number throughout its life-cycle and even in the pteridophyta the only known case of a haploid sporophyte is that of *Nephrodium molle* which was artificially induced to develop in the haploid state from an apogamous prothallus; the spore-formation of this form is not yet known. In animals, on the other hand, apart from artificially induced forms, cases are known where a haploid generation is a normal part of the life-cycle. Strasburger refers to the important work of F. Meves on the spermatogenesis of bees and wasps, which ought to be known to all botanical cytologists. The males are produced from unfertilised eggs in these cases, and so we find no normal first division of the spermatocytes. In the honey-bee this division passes through the prophase and reaches the spindle-stage, but the elements of the nuclear plate do not separate but show regression, while the cytoplasm cuts off a non-nucleate polar-body (Richtungskörper). The first meiotic division, which should be heterotypic, is thus merely a cytoplasmic division; the second division occurs and is of the normal type. Such a case as this indicates the close correlation between fertilization and reduction. In the fact that in these cases the first division (even after the first stages have been passed through) is omitted, but not the second, Strasburger finds support, as will many other cytologists, for the view that these males possess instead of a double series of homologous pangens only a single set. In the absence of a double set the division which separates the homologous ones is excluded. In such cases as this we find additional evidence, though in the nature of the case purely circumstantial, of the importance of the nucleus as the carrier—probably the sole one—of the pangens, and of the probable close relation between segregation and the reduction division.

In the final section of his work, Strasburger reasserts his belief that the nucleus is the sole carrier of hereditary properties and refers again to his very convincing observations in 1908 on the male nuclei of the pollen-tube, which he showed were quite naked and thus could carry into the egg no definite portion of cytoplasm.[1]

In the last few paragraphs very interesting views are put forward on the phylogeny of the nucleus and its relation to karyo-kinesis. The mitotic mode of division is found constantly in the Metazoa and Metaphyta, but not so generally in the lower organisms.

[1] The observations of Godlewski on merogony in echinoderm eggs (which are sometimes quoted against the view that the cytoplasm plays no part in carrying the pangens), Strasburger in agreement with Boveri, does not consider convincing, as the embryos were not reared beyond the early stages.

This is to be explained by the progressive division of labour among the hereditary units in relation to the increasing complexity of the soma. The protoplasm which first appeared on the earth must have been without a nucleus, and with the formative and nutritive functions equally distributed in all its parts. The portions of protoplasm set apart for formative functions were the first hereditary units and they remained at first distributed in the general cytoplasm, as we still find them in certain lower organisms which have no definite nucleus, but only a number of discrete chromatin particles. By the next step they became united in a definite association without being sharply separated off from the general protoplasm, a condition perhaps found in certain bacteria and Cyanophyceæ. In the next stage the units became sharply marked off from the general protoplasm and we have a definite distinction of nucleus and cytoplasm. At this stage the hereditary units, though in part different among themselves, would also be in part the same, *i.e.*, the same purpose would be served by several units. In this condition a division of the nucleus in a relatively simple manner, such as fission, would be sufficient to give a full complement of hereditary units to each daughter nucleus. As the difference, however, between the units increased, till finally the stage was reached in which each hereditary unit had a special function, this mode of division would be clearly insufficient. The qualitative equal division of the nucleus had then to be brought about by the arrangement of the hereditary units (pangens) in thread-like structures; in these threads the units divide and then by the splitting of the thread, a separation of the products of division would be brought about. This mode of division would seem to be the only possible one for the purpose, for otherwise the higher animals and plants would not show so complete an agreement in the process. The necessity for the longitudinal arrangement of the pangens led to the production of chromosomes, and in passing up the vegetable kingdom we appear to find a transition from a large to a small number of these structures; this is well seen in passing from vascular cryptogams to phanerogams. Ferns show very high numbers, while the highest groups of Angiosperms often show exceedingly low numbers. The combination of numerous short threads into fewer longer threads would probably have certain advantages in the formation of the mitotic figure.

The wide range of cytological matters dealt with in this paper and the stimulating nature of the observations and views put forward show clearly that the veteran cytologist still retains unimpaired that mental elasticity—the power to accept and produce new views —which is the mark of intellectual youth.

V.H.B.

THE PHYLOGENY OF THE ARCHEGONIATÆ.

Ueber die Phylogenie der Archegoniaten und der Characeen.

VON DR. HEINRICH SCHENCK (Engler's *Botan. Jahrbuch.*

Bd. XLII., p. 1, 1908).

THIS is one of the most interesting papers that has been published in recent years on the phylogeny of archegoniate plants, and incidentally on the origin of the alternation of generations these plants exhibit. Professor Schenck is mainly concerned with stating the chief facts which lend support to deriving the Archegoniatæ (and also the quite distinct group of the Characeæ)[1] from the Brown Algæ or Phæophyceæ. His paper contains, however, the first clear statement of the idea that the changed environment under which the fertilised egg in archegoniate plants develops, has been a factor of importance in the evolution of the sporophyte. Since this idea, developed on somewhat different lines, was the basis of certain speculations recently published in this journal,[2] it seems desirable that a fuller account of Professor Schenck's paper should be given here than was possible in an article that did not enter into the literature of the subject.

It is convenient to distinguish two aspects of the problem presented by the regular alternation of generations in the Bryophyta and Pteridophyta. One concerns the nature of the ancestral group of plants from which the Archegoniatæ were derived, whether this group is regarded as still existing or as unknown to us. The second concerns the nature of the changes which have led to the type of alternation in Bryophytes and Pteridophytes, and of the factors of importance in these changes. The first is a purely phylogenetic and historical problem, to be attacked on comparative lines; the answer to the second, while largely speculative, may be assisted by experimental studies on existing plants.

Professor Schenck's paper is mainly concerned with the phylogenetic aspect of the problem. He assumes as probable the separate origin of Bryophyta and Pteridophyta from the same group of Thallophyta, and in the absence of direct evidence afforded by intermediate forms, discusses the question " To which group of Algæ we should attach them ? " He criticises and dismisses as improbable the views that *Coleochæte* or any other oogamous Green Algæ represent the ancestral forms, and similarly dismisses the Rhodophyceæ. He then proceeds to examine the evidence in favour of the assumption of a genetic connection of the Archegoniatæ with the Phæophyceæ. This is done under four heads, and mention of these, with a few remarks, will show the nature of the evidence upon which Professor Schenck relies, without, of course, fully indicating its scope.

[1] The part of the paper dealing with the Characeæ will not be considered further.

[2] New Phytologist, Vol. VIII., No. 1.

In the first place a detailed comparison is made of the sexual organs of the Archegoniatæ with the gametangia of the Brown Algæ. The wall of cells limiting the antheridia and archegonia and the canal cells of the latter are regarded as adaptations to terrestrial life. Proceeding to the reproductive organs of the spore-bearing generation, the spore-mother-cells of the archegoniate plants are compared with the unilocular sporangia of the Phæophyceæ and especially of the Dictyotaceæ. While the essential correspondence of the tetrads in the two cases will readily be granted, it is not so easy to regard as necessary, or probable, the assumption that the structures corresponding to the sporangia of the Algæ have become endogenous in the Archegoniatæ. This is regarded as having taken place as an adaptation to terrestrial life. The archesporial layer in the moss-sporogonium is compared to a sorus of sporangia (such as are borne on the thallus of *Padina*) become endogenous. This assumption leads to the amphithecial archesporium and the presence of a columella in *Anthoceros* being regarded as relatively primitive characters, a view against which serious objections could be urged. What are usually known as the sporangia of Pteridophyta are regarded as special appendages of the sporophyte enclosing numerous endogenous " sporangia," and Professor Schenck. proposes to call the whole structure not a sporangium, but a spore-sac (Sporentheka).

In the next section of the paper the gametophyte of the Archegoniatæ is compared as regards form and organisation with that of the Brown Seaweeds. The points of comparison are all general ones such as distinction of a basal attaching region and the differentiation of the branches of the thallus. The most that can be concluded is that comparison of body-form and structure is easier between the Archegoniatæ and the Brown Seaweeds than between them and other existing Algæ. This criticism applies even more strongly to the comparison of the sporophyte of archegoniate plants with the thallus of the Phæophyceæ, and little weight can be attached to the parallel of foot and upper region in the embryo with the attaching disc and upper portion of the thallus in a Brown Seaweed.

While the lack of any definite homologies between the gametophyte of the Archegoniatæ and the thallus of the Brown Seaweeds is a serious difficulty in assuming a genetic connection between the groups, the absence of points of comparison between the free-living sporophyte of the Brown Algæ and the sporophyte of the Archegoniatæ can be explained. This difficulty is met by considering the different and quite new conditions of development which affect the fertilised egg when retained in the archegonium. Professor Schenck does not consider this influence in great detail, but he states it very clearly, both in the introduction and in the portion of the paper dealing with the origin of the sporophyte. He shows also that the difference between the heteromorphous alternation of the Archegoniatæ and the homomorphous alternation of similar individuals in *Dictyota* finds its explanation in this factor. He further suggests that owing to this change in developmental condition of the egg the origin of the differences between sporophyte and gametophyte may have been sudden. The importance of this factor as bearing on the difficult problem presented by alternation of the heteromorphous

type is obvious and its clear statement gives this paper an important place in the literature of this subject.

The outcome of the detailed comparison of archegoniate plants with the Brown Algæ, which is the main purpose of the paper, is thus not conclusive. It yields no homologies which force us to assume a genetic connection between these groups. No organ or structure is so similar that it is likely to have been derived by descent and unlikely to be of independent origin. To dismiss the peculiarities of the sexual organs and sporangia as adaptive only emphasises the absence of the resemblances which we might have expected to find in ancestral forms of the archegoniate plants. Professor Schenck has collected in a most useful form the case for the Phæophyceæ as direct ancestors of the Archegoniatæ, and has freed the comparison from some unnecessary assumptions made by Potonié and Hallier. The value of the statement of the case is not diminished even if we conclude that at present there is no clear evidence as to which group of the Algæ were ancestors of archegoniate plants, or as to whether any existing forms closely resemble the unknown ancestors.

<div align="right">W.H.L.</div>
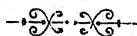
RECENT ADVANCES IN THE STUDY OF HEREDITY.

(A Course of Lectures, for the University of London, delivered in the
Summer Term, 1909).

By A. D. DARBISHIRE.

LECTURE III.

THE MENDELIAN HYPOTHESIS.

NOW we pass from the bright daylight of demonstrable fact into the dark and dangerous alleys of inference. It may be objected that my metaphor is ill-chosen, inasmuch as, in this instance as in most others, the inferences drawn from the facts are not merely as clear as, but more illuminating than, the facts themselves. My answer to this is that the seeming brightness of the region of hypothesis is precisely the danger I wish to guard against. It is just because the alleys of inference do not seem dark that they are so dangerous. We are too apt to forget that there is no other light in them than that shed by our own imaginations; in other words that the order, which we believe we have detected in one of nature's workings, is the product of our own imaginations and is projected by us into them, to be subsequently "discovered" as we fondly imagine, as a new "law."

Let us therefore during this lecture keep vividly before our minds the fact that we are in the region of hypothesis and that in order to reduce our deceit of ourselves to as low a minimum as possible, we must maintain an attitude of continual distrust of ourselves whilst in that region. Our self-deceit can be reduced by making it a practice to infer only a very short distance ahead of the facts; to refrain from proceeding to further inferences until the last one has been established by experiment and observation; and

to remember that the question we have to ask ourselves, in considering the evidence relating to any thesis, is not "how many facts support it?"; but "is there a single one which is against it?"

Mendel's hypothesis is a very simple one, and explains so large a number of otherwise anomalous phenomena, that we should from the outset adopt an extremely critical attitude towards it.

Let us deal with the interpretation of the phenomena, part of the evidence for which we considered in detail. There is no observable difference between the germ-cell which, if it unites with its like, gives rise to a green Pea and one which, if it unites with its like, gives rise to a yellow. Yet we cannot but believe that there is something in the one which represents the green colour and something in the other which represents the yellow. We may call these things for simplicity of expression the green-factor and yellow-factor respectively.

Mendel's theory related primarily to the condition of the germ-cells of the hybrids with respect to these factors. He supposed that half of them bore the green and the other half the yellow factor. He further supposed—and the burden of proof, of course, rests with anyone who supposes the contrary—that in fertilization these germ-cells mate at random, that is to say without reference to the colour-factors which they contain. The result, on these hypotheses, of the union of the germ-cells of two hybrids would be the following four types of union, which would occur with equal frequency if the number of germ-cells concerned were a large one. (By G is signified a germ-cell containing a green factor; and by Y one containing a yellow).

$$Y \times Y = \text{Yellow.}$$
$$Y \times G = \text{Yellow.}$$
$$G \times Y = \text{Yellow.}$$
$$G \times G = \text{Green.}$$

Now it is supposed that the pure-breeding yellow produces only yellows, when mated with its like, because it only contains germ-cells bearing the factor for yellowness, and that the pure green breeds true for a similar reason; and we know, if this hypothesis is correct, that the result of the union of a germ-cell containing the yellow factor with one containing the green is a zygote (as the product of the union of two germ-cells is called) bearing the yellow character. Therefore the results of the four types of unions will be what are written to the right of them, namely three yellows and one green. But it will, of course, immediately be seen that of

these yellows there are two types; one of which is the result of the union of two germ-cells, both bearing the yellow factor; the other of which is the result of the union of a germ-cell bearing the green factor with one bearing the yellow. The former type evidently corresponds to the (pure) yellow in F_2 which breeds true, the latter to the (hybrid) yellows whose offspring split up again into yellows and greens. And, inasmuch as, on this hypothesis, the greens present no difficulty, it will be seen that this theory is in perfect accord with observed results.

Furthermore, the otherwise anomalous fact that the yellow hybrids continue to produce yellows and greens in the same proportions as we proceed away from F_1, is explained; for, on this theory, the result of the union of two individuals is determined by the contents of the germ-cells borne by them; and the gametic constitution of the hybrid in F_{10} is identical with that of the F_1 hybrid. It is not necessary to point out in detail how all the other results which ensue from the union of germ-cells which differ in respect of a single pair of characters (in this instance, yellow and green) are in accord with Mendel's theory; but it is worth while casting a glance at the basis on which the Mendelian prediction as to the result of the crucial experiment described on p. 177 rests. No difference between the result in F_2 of the union between a pure yellow and a *pure green*, and a union between a pure yellow and an *extracted green in F_5* would be anticipated on the Mendelian hypothesis, because the contents of the germ-cells of a pure green and those of the germ-cells of an extracted green in F_5 are exactly the same, namely the green factor, and the green factor only.

Before proceeding to a further consideration of this question of gametic constitution, let us pay attention to a feature of Mendel's theory, which is so essential a part of it, that it is apt to be overlooked. It is that the theory is essentially a germinal theory of inheritance: it starts by assuming the existence of certain potentialities in the germ-cell and is in no way concerned with the question as to how they got there. It is a theory, therefore, which anyone who holds a Lamarckian theory of evolution must reject, unless he maintains that the conception of the relation between successive generations of organisms which that theory involves is not applicable to certain characters, of which cotyledon-colour in *Pisum* is one; or that the Mendelian experiments have not yet been continued for a number of generations sufficiently great to allow the machinery of inheritance, postulated by that theory, time to exert any measurable effect. This

"germinal" feature is shared by Weismann's theory of inheritance; and is the most salient characteristic of the modern so-called neo-Darwinian view of inheritance. The question whether we should associate it with Mendel's, or Weismann's, or anybody else's name has little interest for me; but the reader who is curious on the point will find it briefly discussed in my first lecture.

It has become customary to write the four possible types of union of gametes, and the zygotes resulting from them, in such a case as that which we have been considering, as follows:—

$$Y \times Y = YY$$
$$Y \times G = YG$$
$$G \times Y = GY$$
$$G \times G = GG$$

The formulæ to the right of the equation marks may signify either the nature and number of the gametes borne by the zygotes produced by the union of the gametes to the left of the equation marks, *or* the somatic constitution of these zygotes themselves. The latter signification is preferable, because the former, by omitting the zygote altogether, commits one to a too dangerously unconditional belief in the theory of the continuity of the germ-plasm; and because the latter serves to lay emphasis on one conclusion reached by Mendelian analysis which is in accordance with cytological knowledge. I refer to the conclusion that the zygote is a double structure whilst the gamete is a single one, which is in accord with the well-known fact that the number of chromosomes in the zygote is twice the number in the gamete.

A very simple way of illustrating the results of the union of the gametes of two hybrids is to place in each of two hats, say, a hundred white and a hundred red counters, and a similar lot into another hat. The random union of the gametes can be imitated by drawing pairs from each hat, with eyes shut, and placing them in separate rows according as whether they are Red-White, Red-Red, or White-White pairs. The red counters may be placed on the top of the white ones to illustrate the dominance of red over white. The result will, on the average, be 25% RR, 50% RW and 25% WW. The two kinds of zygotes which are produced in such a cross can be well illustrated by the means of these counters. A zygote which is the result of the union of similar gametes, *i.e.*, a "red" with "red," or "white" with "white" is called a *homozygote*; of this there are two kinds, one in which both gametes are recessive, the other in which both are dominant.

A zygote which is the result of the union of dissimilar gametes is termed a *heterozygote*.

The number and nature of zygotes formed from the random union of gametes of known contents can also be—and I think most conveniently—represented in tabular form as follows :—

	♂ Y	G
♀		
Y	YY	YG
G	GY	GG

The figures at the top of the table relate to the two kinds of male gametes; those to the left of it, the two types of female gametes; and the four zygotes produced are given in the four squares of the table. It is customary to limit the use of such a table to the representation of the result of matings in which more than two characters are concerned; but it is advisable to be familiar with its use for a single pair of characters, because the application of Mendelian analysis to the interpretation of certain phenomena of the inheritance of sex can be much more clearly illustrated by means of such a four-square table, than by any other means.

We may now proceed to consider the results of the unions between the various zygotic types; and, in considering these, it will be convenient to designate the dominant members of such a pair of characters as yellow and green by D and the recessive by R. There are thus three zygotic types, DD, DR and RR. The following is a list of the various unions in which these types may take part, together with their results.

					Percentage Numbers of :—		
					DD	DR	RR
a.	DD	×	DD	=	100 ...	— ...	—
b.	DD	×	RR	=	— ...	100 ...	—
c.	DD	×	DR	=	50 ...	50 ...	—
d.	RR	×	RR	=	— ...	— ...	100
e.	RR	×	DR	=	— ...	50 ...	50
f.	DR	×	DR	=	25 ...	50 ...	25

We have already considered all of these with the exception of c and e, *i.e.*, the union of the heterozygote with the dominant and with recessive homozygote respectively. As will be seen from the table the results in both cases are equal numbers of the two types mated. I wish to lay stress on this type of mating, because of the important

part which it plays in the interpretation of sex-inheritance and also because familiarity with it is necessary for an understanding of an experiment which I shall now proceed to describe.

We have spoken a great deal about the characters of an organism being determined not by the somatic characters of its parents and ancestors, but by the potentialities existent in the two germ-cells which give rise to it; but we still speak loosely of "mating two individuals"; and it is very important that we should make our conception as to what we mean by such a statement perfectly clear. Now if it is really the case that the characters of a zygote are determined solely by the potentialities existent in the gametes which by their union give rise to it, the characters of the parents which produce these gametes should be immaterial; and if we were to isolate a green gamete and a yellow one and allow them to conjugate the result should be the same as the result of the union of a green gamete borne by a green Pea and a yellow one borne by a yellow Pea. It is not possible to do this; but it is possible to do what is far more striking, and that is to witness the result of the union of a gamete bearing the D character with one bearing the R character, when both gametes are produced by parents exhibiting the D characters.

This I have effected, not with the pair of characters yellow and green in the cotyledons of *Pisum*, but with another character of the cotyledons, namely their shape. This pair of characters was, as is well known, the first on the list of seven characters with which Mendel himself dealt in his classical experiments. The two characters are round and wrinkled, of which round is dominant, wrinkled recessive; segregation occurs, so far as the evidence goes, according to exactly the same scheme as that to which the cotyledon colour-characters conform.

When we cross a round with a wrinkled Pea we are of course merely bringing together a gamete bearing the factor for roundness and one bearing the factor for wrinkledness. But because we invariably do this by transferring pollen from a plant whose first two leaves, or cotyledons, were round, to the pistil of one whose cotyledons were wrinkled (or *vicè versâ*), we are apt to slide unconsciously into the belief that the characters of the actual parents have something to do with the result. Now in the mating which I am about to describe, the round gamete was borne by a plant whose cotyledons were round (*i.e.*, by a round zygote), *and so also was the wrinkled gamete*; only, of course, the round zygote in

the first case was of constitution DD, whilst that of the second was DR. The mating was of this nature:—

DD × DR; giving 50% DD × 50% DR.

Our interest centres on the DRs produced; and we find that the result of their self-fertilization is the production of rounds and wrinkleds in the same proportions as those which obtain in the F_2 resulting from a union between a round gamete borne by a round zygote and a wrinkled gamete borne by a wrinkled zygote.

What makes this case more remarkable is the fact that the heterozygote round which bore the gamete with the wrinkled factor was not an F_1 heterozygote, but an F_5 one. That is to say the wrinkled zygotes which appeared in normal proportions in the F_2 from the cross in question had no wrinkled individuals in their ancestry nearer than the great-great-great-great-great-grand-parental generation.

This particular cross was made without deliberate intention by the same pollinations which were designed to effect the cross between the pure yellow and the extracted green in F_5 described in my last lecture. The F_5 greens used in that experiment had been saved from three distinct plants, all of which were of course heterozygous in respect of cotyledon colour. With regard to cotyledon shape, two happened to be dominant homozygotes the other a heterozygote. When I was recording the F_2 from this cross (between pure Y and extr. G in F_5) I was at first puzzled when I found that many of the plants bore wrinkled as well as round seeds; indeed, so far was I from understanding the interest of the case that at first I contented myself with recording the fact of the plants being heterozygous and did not count the actual numbers of rounds and wrinkleds. That the Mendelian interpretation of the case which I have suggested is the true one cannot, I think, be doubted: for it was found that all the crosses which had given wrinkleds in F_2 were made with the heterozygote round referred to above. I am aware that it can be urged that there is nothing very remarkable in this experiment and that the same thing is illustrated equally well, if not better, by the fact that a wrinkled zygote is formed by two wr. gametes both of which are borne by zygotes, *both* of which are round, in the mating DR × DR. But the ordinary Mendelian cross is so familiar now, that it is difficult to illustrate unfamiliar ideas by its means. I give below the pedigree (B) of this cross together with that of the cross described in my last lecture (A); in both cases the somatic characters of the

individuals are written to the right of the circles, whilst their zygotic constitutions are written inside them.[1]

PEDIGREE A.   PEDIGREE B.
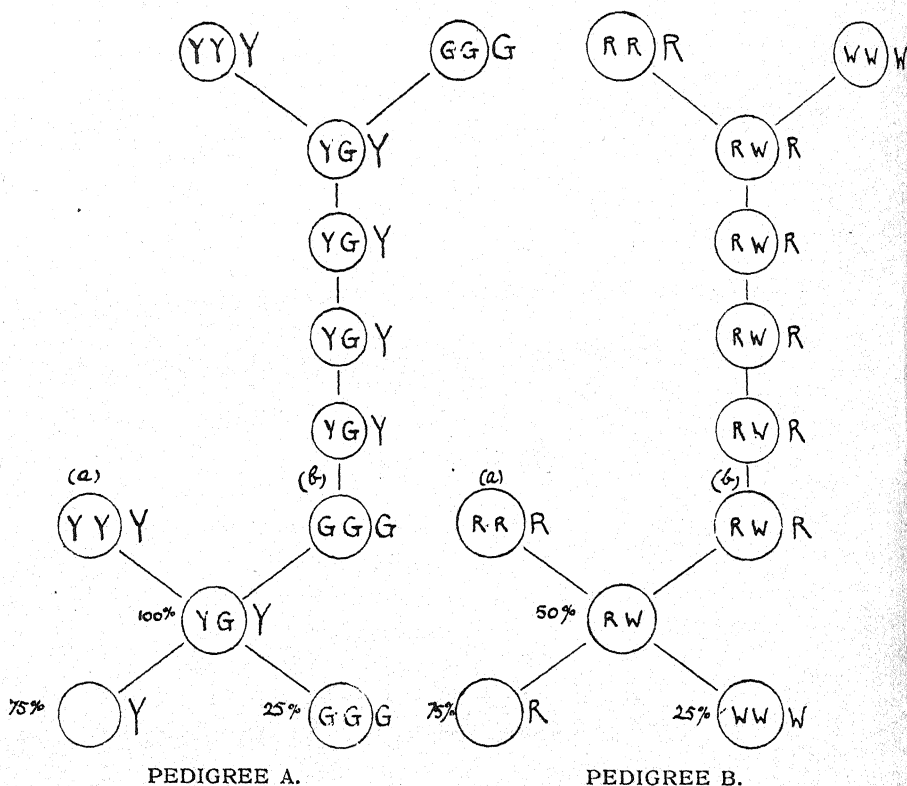
The difference between cross *a* and *b* in pedigree A and *a* and *b* in pedigree B is that whilst in pedigree A the two zygotes crossed actually bear the D and R characters respectively, in pedigree B both zygotes bear the D character.

After this digression into that part of Mendelian theory which is common to it and to Weismann's and to all "germinal" theories of inheritance, let us turn to the consideration of the new ideas for the introduction of which Mendel is solely responsible. But, before we do so, let me insist for the last time on the importance of carefully discriminating in what is called Mendelian theory between those sections of it which are common to Weismann's, and indeed to the whole modern conception of inheritance, and those sections to which alone the title Mendelian should be applied.

[1] The details of this experiment will be found in Proc. Roy. Soc. B., Vol. 81, p. 70.

The question to which I now propose to direct your attention is a Mendelian one in the proper sense of that term. It will have been gathered from the description of the phenomena which has been given, that the characters which behave in a Mendelian fashion in inheritance are associated together in pairs, of which one member is dominant and the other recessive. Such characters, which behave as independent units in inheritance in the manner described above, are termed unit characters; and also, in view of the fact that every such character has its counterpart, which is either dominant or recessive to it,—*allelomorphs*. The adjectival form of this term is useful; because we can express the fact that round is one of the two members of a pair of characters, of which the other is wrinkled, by the statement that round is *allelomorphic* to wrinkled.

We have so far confined our attention to crosses in which the two individuals mated differed in respect of a single pair of characters only. Now let us proceed to the consideration of one in which the two individuals mated differ in respect of two pairs of characters; for instance—not to leave *Pisum*—a cross between a yellow wrinkled and a green round pea. The actual result is given in the following scheme.

$$\text{YW} \times \text{GR}$$

F_1 YR

F_2 9YR   3YW   3GR   1GW
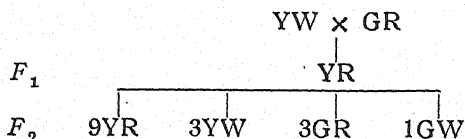
A cross involving the same two pairs of characters might have been made by crossing a YR by GW; and the result in F_1 and F_2 would have been the same. But it is better to make the cross in the way represented in the above table because the fact is brought out that the matter of dominance is absolutely independent of the individuality of the parent which bears the dominant character. The result of a cross between a YR and a GW does not tell us that the dominance of the two characters Y and R is not an attribute of the individual which manifests them; but the result of a cross between a YW and a GR excludes the possibility of such an interpretation. The result in the two cases is, of course, the same; but in the former case both dominant characters are borne by one parent; whilst in the latter each of the two parents bears one of them.

The result in F_1 and F_2 of the cross we are considering follows from the knowledge which already we possess of the mode of

inheritance of the two pairs of characters involved, considered separately. We know that Y is dominant to G; and R to W. We know that in F_2 we get the proportions, in the one case 3Y : 1G; and in the other 3R : 1W. We should therefore expect to get on the average, in every 16, 3 × 3=*9* YR; 3 × 1=*3* YW; 1 × 3=*3* GR and 1 × 1=*1* GW.

These proportions are found to obtain in experimental results. I quote the results obtained by Mendel and Bateson.

	YR	YW	GR	GW
Mendel	315	101	108	32
Bateson	4926	1656	1621	478

It is customary to deduce these proportions from the contents of the gametes of the hybrids. It is evident, if we start with the assumption that a gamete can only bear one member of a single allelomorphic pair, but can be the bearer of any number of characters, so long as they belong to distinct allelomorphic pairs, that in the hybrids in question four kinds of gametes will be produced in equal numbers; namely YR, YW, GR and GW. If one is asked why gametes with the formula of YG or RW or even RR cannot exist; the only answer which can be given at the point which we have now reached is that it is a part of the Mendelian theory (sometimes referred to as the doctrine of the " purity of the gamete ") that a gamete cannot bear both members of the same allelomorphic pair. This is of course not a satisfactory answer. But we shall see, at a later stage in the argument, that a satisfactory answer can be given.

The manner in which the result in F_2 is brought about by the random union of the four kinds of gametes named above may be represented by a table similar to that on page 247. The four types of gametes borne by the male are written at the top, the four borne by the female at the left-hand side. The various types of the zygotes produced are given in the sixteen squares of the table; below these formulæ are written in italics, in each square, the somatic characters of these various zygotic types.

It follows from the Table that only one of the 9 YRs are homozygous (DD) in both respects, *viz :* that in square *a*. Two are heterozygous (DR) for colour, but DD for shape, *viz : c* and *i*. Two are DD for colour, but DR for shape, *viz : b* and *e*. Whilst four are DR in both respects, *viz : d, g, j* and *m*.

In the case of the 3 YWs and 3 GRs; the W and the G in both cases are of course RR.[1] But of the 3 YWs the Y in two cases is

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[1] It is, perhaps, hardly necessary to warn the reader not to confuse RR signifying Round-Round with RR signifying Recessive-Recessive.

DR, *viz :* h and n, and in one DD, *viz : f*; and of the 3 GRs the R in two cases, *viz : l* and o, is DR and in one, k, it is DD.   The zygote

♂	YR	YW	GR	GW
♀ YR	*a* YY·RR YR	*b* YY·RW YR	*c* YG·RR YR	*d* YG·RW YR
YW	*e* YY·RW YR	*f* YY·WW YW	*g* YG·RW YR	*h* YG·WW YW
GR	*i* YG·RR YR	*j* YG·RW YR	*k* GG·RR GR	*l* GG·RW GR
GW	*m* YG·RW YR	*n* YG·WW YW	*o* GG·RW GR	*p* GG·WW GW

which bears two recessive characters, the GW (square p) is of course homozygous in both respects.   It may be noted that the zygotes which are homozygous in respect both of colour and of shape, lie along a diagonal which traverses the Table from the top left to the bottom right corner ; whilst the zygotes which are heterozygous in both respects lie along the other diagonal of the Table.

I think it is desirable to note in passing, that although these various zygotic types follow from the theory with which we started in constructing the Table, they can also be deduced from a knowledge that in the case of cotyledon colour and shape there occur in F_2 three types of individuals, in each case a pure one bearing the dominant character—Y, a hybrid one with the same character—(H) Y, and a pure recessive type—G.

If the two following series of characters, a and b, in the

$$a. \quad 1\ Y \quad 2\ (H)\ Y \quad 1\ G$$
$$b. \quad 1\ R \quad 2\ (H)\ R \quad 1\ W$$

numerical proportions indicated, be distributed at random over a number of individuals in such a way that each individual may bear any two characters so long as they are not two of the same or the two members of a single allelomorphic pair, the numerical pro-

portion in which the various types of individual will occur will be as follows :—

	a.		b.		c.		d.
Y·R	1	Y·W	1	G·R	1	G·W	1
(H)Y·R	2	(H)Y·W	2	G·(H)R	2		
Y·(H)R	2						
(H)Y·(H)R	4						
	9		**3**		**3**		**1**

Each of the numbers in the columns *a*, *b*, *c*, and *d* in the second Table is arrived at by multiplying the figures to the left of the two characters, in the first table, which are borne by each zygotic type in the second.

The fact that not only the distribution 9 YR, 3 YW, 3 GR, 1 GW, but the various zygotic types within 3 of these categories, can be deduced from data other than the nature of the contents of the gametes concerned in producing this assemblage of forms is of no small importance; because it takes the ground from under the feet of any advocate of the Mendelian hypothesis, who might argue that it was highly improbable that a theory, which accounted not only for the proportion $1:2:1$, but for the complex condition of affairs involved in the proportion $9:3:3:1$; and subsequently for the proportions $9:3:4$ and $9:7$, could be unsound. Let me express what I mean in another way. The Mendelian advocate might argue thus: "It may be that the theory suggested by Mendel is not the true explanation of the results it is designed to explain; and that it is a pure fluke that the agreement between hypothesis and experimental results is so close. I think this highly improbable, but I am ready to admit that this may be so. But surely, if starting with this theory, we can go on to explain the proportion $9:3:3:1$ and $9:3:4$, it is inconceivable that the theory from which we started is not the true explanation of the $1:2:1$ proportion." The fallacy in this argument is that the $9:3:3:1$ ratio, although, of course, it *can* be deduced from the 16-square Table, follows merely from the $3:1$ ratio; and, not only so, but the various zygotic types within the categories can be deduced from the $1:2:1$ ratio. My present belief is that Mendel's theory is very close to, if it is not actually the true explanation of the phenomenon of segregation; but I think it is important to realise that the fact that the $9:3:3:1$ ratio, and others which follow from this ratio, can be deduced from this theory, is no *more* a proof of its truth than the fact that the $1:2:1$ ratio is consistent with it.

ON A CONE OF *CALAMOSTACHYS BINNEYANA* (CARRUTHERS) ATTACHED TO A LEAFY SHOOT.

By H. Hamshaw Thomas, B.A.

(Downing College, Cambridge).

[With Plate I. and Text-Figs, 31, 32.]

ALTHOUGH forty years have now passed since the first decription of the cone *Calamostachys binneyana* was published, hitherto no petrified specimen has been found in connection with vegetative organs of any kind. It may therefore be of some interest to record the discovery of a specimen showing a cone with four whorls of Calamite leaves attached at the base.

The specimen was found in a calcareous nodule from the Halifax Hard Bed of the Lower Coal Measures at Huddersfield. I received three longitudinal sections cut through it from Mr. J. Lomax on December 8th, 1908.

Historical. Before describing the specimen, a brief review of the previous work published on the subject will be given. The first account of an English cone of this type was by Carruthers,[1] who called it *Volkmannia Binneyana*. He gave a brief description of its structure, comparing it with *Volkmannia Ludwigi*, previously figured in 1861.[2] He terms the sterile bracts between the sporangiophores foliage leaves, apparently without much evidence as to their structure or homologies. It will be shown later that there is really considerable similarity between the two organs.

In 1868, Binney[3] published a number of excellent figures of transverse and longitudinal sections of a cone which he attributed to *Calamodendron commune*, and gave a brief description of them. As in almost all the other species described, the base of the cone was not seen.

Schimper[4] introduced the generic name *Calamostachys* for cones similar in type to that figured by Binney. He stated however that Binney's strobilus was distinct from the cones of *Calamodendron commune*. In his excellent figure, the top of the cone, and probably the base, are shown, but neither the stem nor the leaves below the base are indicated.

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[1] Carruthers (67).   [2] Ludwig (61).

[3] Binney (68), p. 23, Pls. IV. and V.   [4] Schimper (69), p. 330.

Our knowledge of the detailed structure was greatly extended by Williamson[1], who figured and described many specimens in his Memoirs. All the preceding authors had unhesitatingly attributed *Calamostachys* to a *Calamite* stem, but for a long time Williamson considered that it was not the cone of a true *Calamite*, but rather allied to *Asterophyllites* (*Sphenophyllum*) or *Lepidodendron*. This conclusion was disputed by Hick[2] in an important contribution. He described the cone in detail and drew attention to the layer of cells in the bracts, the lumina of which were occupied by dense masses of black, carbonaceous substance. He noticed that a tissue of this kind was present, both in young stems and leaves of *Calamites*.

Finally, in 1894, Williamson and Scott worked through all the material again, practically settling the question of the affinities of the cone and giving an excellent account of its anatomy. They conclude with the following statement: " In view then of the fact that a renewed examination of *Calamostachys binneyana* has tended to show that its anatomy is much more similar to that of *Calamites* than was formerly supposed, while another species of the genus has an exactly similar structure, we think that the relation of our British species of *Calamostachys* to *Calamites* may well have been a close one. It is even possible that some of the stems which have been described under the general name of *Calamites* may have been those on which *Calamostachys* fructifications were borne. Beyond this we cannot go until further evidence of continuity has been produced . . . . . The solution of the problem must await further evidence." [3] Though in the present specimen I have been unable to get a section passing through the stem below the cone, yet the occurrence of *Calamite* leaves which were undoubtedly attached to it, is certainly part of the evidence required.

Description of the Specimens. The material at my disposal consists of three slightly oblique, longitudinal sections through the cone. One of them (No. 3) only contains a small portion of the upper part. The section (No. 1) shown in Pl. I., Fig. 1 is nearly radial through the base of the cone, becoming tangential above and below. The other section (No. 2) is cut tangentially to the cone at its base, and shows the axis of the upper portion.

The length of the cone (Fig. 1) was at least 14 mm., and its greatest breadth about 5 mm. It seems to have been cylindrical in shape. Eight whorls of fertile appendages and as many sterile

[1] Williamson (73), (80), (81), (89).   [2] Hick (93).
[3] Williamson and Scott (94), p. 919.

are seen. The axis does not present any unusual features. The number of sporangiophores in a whorl cannot be made out in the absence of transverse sections, but it seems to have been about the usual number, and their form and arrangement were normal. The sporangium walls are seen in several places, but it is not possible to determine the number of sporangia present on each sporangiophore. Apparently most of them had dehisced before preservation took place, and only a few spores are seen which show no signs of heterospory.

The bracts are of the usual type, some of them are very well preserved and show several interesting features. The exact number in the whorl cannot be accurately determined, but it was probably approximately double that of the sporangiophores. They are united at the base into a disc, about 3 mm. in diameter, and on becoming free turn sharply upwards; their free portions are 1—2 mm. in length. Each has a small vascular bundle which is seen in transverse section near the axis in Text-fig. 31. Its centre is
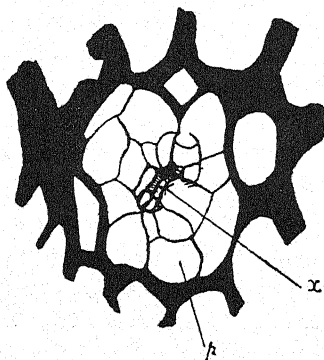
Text-fig. 31. Transverse section, near the axis, through the vascular bundle of a bract. *x*., Small xylem tracheides in centre. *p*., Clear thin-walled cells (phloem), surrounded by thick-walled cells of cortex and disc. × 250.

occupied by a group of very small xylem tracheides, and this is surrounded on all sides by thin-walled cells. It seems not unlikely that the latter tissue is phloem, and, consequently, the bundle may have been concentric, and not collateral as formerly supposed. It should be remarked, however, that we have no means of finding out whether the thin-walled cells were really phloem, and it is possible that true phloem was absent from the bundle.

The tissue of the disc is differentiated into two parts, that at the base of the bracts consisting of clear cells with thin walls,

while that between the bracts is composed of large dark cells with
thick walls (see Text-Fig. 31). On the adaxial side of the bundle
a strand of sclerenchymatous fibres arises, which increases largely
in bulk towards the apex of the bract, and forms the greater part
of its free portion. On the other side, a layer of parenchymatous
cells is seen, many of which are characterised by the dense black
contents noticed by Hick. This tissue arises near the point where
the bracts become free and increases in amount towards the apex.
A layer of rudimentary pallisade tissue, very similar to that found
in the leaves, forms the outer portion of the free bracts. This is
usually badly preserved, and is only seen in a few places. A thin
epidermis is also present. In this specimen the bracts of successive
whorls seem to have only slightly overlapped one another.

The lowest whorl of the cone apparently consists of bracts,
and differs from those above it in a greater development of the thin-
walled parenchymatous tissue in the disc, which is thus a little
thicker, while its diameter is smaller. There is also a better develop-
ment of pallisade tissue in the free parts of the bracts, and altogether
they bear still closer resemblance to the leaves. Separating this
whorl from the highest of the leaves, there is, however, a whorl of
peculiar lateral organs (*a*) seen in Fig. 2. Unfortunately the only
slide in which this is seen is not very well preserved in this region,
and it is difficult to come to any certain conclusion as to the nature
of this whorl. The tissue consists of large cells, not conspicuously
thickened, and with little definite arrangement. In one place there
is a group of rather elongated cells with one or two xylem tracheides.
We may see here simply the fused bases of a whorl of leaves, but
there are several reasons for believing that this is not the case.

Slide No. 2 is cut tangentially to the cone in this region, and
passes through the outer portion of the disc of the lowest whorl
of bracts. Some of the members of the highest whorl of leaves are
well seen, but between them and the disc, in the position of the
tissue now in question, there are no traces of leaves, nor of any
other organs.

An examination of the external edge of the tissue shown in
Fig. 2 leads to the conclusion that this whorl was simply a disc of
parenchymatous tissue. Again, there is no indication of a leaf-
or bract-base cut through transversely, but this argument is not
conclusive owing to bad preservation.

It may be suggested then that we have here a whorl of appen-
dages differing from the bracts, leaves, and sporangiophores, and

possibly equivalent to the annulus of the cones of modern Equisetums.

The leaves. Below the "annulus" four whorls of leaves are seen cut through in tangential section (see Fig. 3). In the highest whorl parts of three leaves are seen. The same number appears in the second and third whorls, while the number in the fourth is rather uncertain. The leaves were not united at the base, and a certain amount of displacement had taken place prior to preservation. The members of successive whorls alternate in position. In slide No. 2 the leaves are seen cut through more transversely, and four leaves are seen in the second and third whorls, while the three leaves in the first appear to alternate in position with the lowest bracts. I do not propose to give a full account of the structure of these leaves here; they will be reserved for a subsequent paper on the leaves of *Calamites.* They were, however, small linear structures 2·5—3·5 mm. long, ·75—1 mm. broad, and crowded together so that four whorls occupied a length of about 2·5 mm. of the axis. Further away from the cone the distance between the whorls increases. The number of leaves in each verticel cannot be determined, but it was most probably the same as the number of the bracts.

In structure they closely resemble the bracts, but differ in being quite free, and also in the relative proportions of the fibres and pallisade tissue. The amount of sclerenchymatous tissue decreases somewhat as we pass away from the cone, as we should expect when we remember that the function of the bracts must have been chiefly protective.

The leaves differ somewhat in structure from those previously described.[1] A large strand of fibres runs along the whole length of the leaf (*s.* Fig. 3). The vascular bundle lies below this and is very small. On the lower side of the leaf we next have a layer of the elongated parenchyma, cresentic in transverse section, with dense black contents, and running the whole length of the leaf. Hick[2] applied the term "melasmatic tissue" to cells of this kind, and it seems convenient to retain this term provisionally. This layer is succeeded by a zone of pallisade tissue, composed of radially elongated cells with large intercellular spaces. On the outside there is a narrow epidermis. The stomata were small and are only seen in a few places.

From the size, shape, and arrangement of the leaves it may be concluded that they were of the type known from impressions as *Calamocladus (=Asterophyllites) grandis* (Sternb).

¹ Hick (95).   ² idem.

On the axis between the leaf whorls there are a large number of minute black bodies, seen in transverse section in Fig. 3 and Text-fig. 32 C, where their shape is very irregular but flattened. They also occur on the base of the cone and on the fertile portion, as seen in Fig. 2 and Text-fig. 32 A and B, which show them in longitudinal view. In many cases the black portion has shrunk away from the wall and forms an irregular band in the centre. It has a very similar appearance to that characteristic of the

Text-fig. 32. Hairs at the base of the cone. A, Group of hairs on axis near base of lowest sporangiophore. ×60. B, Hairs on lower side of "annulus." ×60. C, Transverse section of group between leaf bases. ×120.

"melasmatic tissue." These bodies appear to have been of the nature of small hairs, and from their dense contents may, perhaps, have been glandular. Their occurrence is of some interest, as hitherto hairs have never been noticed on any of the Calamites, and they are very rare on recent Equisetums, if indeed they occur at all.

Leaves of the type described above have been also found in connection with young twigs, and it seems probable that before long they will be found attached to a well preserved stem. The question of the affinities and stem of *Calamostachys binneyana* will then be finally set at rest.

Impressions of Calamostachys. In the Sedgwick Museum (Cambridge) there are several slabs of shale from Raven Shore, Lancashire, collected from the Brooksbottom seam by Mr. Aitken[1]. They show a large number of impressions of cones and small leafy shoots of *Calamites*, together with some larger stems. The cones correspond very closely with that just described, and probably belonged to the same species. A typical example is shown in Fig. 4.

[1] One of these specimens was figured by Binney, *ibid*, p. 27, Pl. VI., Fig. 1.

Their length appears to vary considerably, from 15 to 35 mm. or more, but it is very difficult to determine if they are complete. They seem to have been cylindrical in shape with a blunted apex. The breadth is 4—5 mm., and there are six or seven whorls of sporangiophores per centimetre.

Below many of the cones a leafy stem is seen, often several centimetres in length. It is about ·8 mm. broad and is densely covered with small falcate leaves, 6 or 7 whorls occurring in a length of 3 mm. Each leaf is about 2·5 mm. long. The preservation of the specimen does not allow the number of leaves in a whorl to be accurately counted, but it seems to have been considerable. The " annulus " cannot be made out.

Numerous small, leafy branches without cones also occur, bearing similar whorls of, perhaps, 8—10 leaves. The larger stems have internodes more than 1 cm. long, and bear rather longer leaves.

These cones have been identified as *Paracalamostachys williamsoni*, Weiss, and closely resemble the type specimen described and figured by Weiss.[1] In the latter,[2] which is now in the British Museum (Nat. Hist.), the leafy shoots below the cones are considerably shorter than in the present case, but they differ greatly in length among themselves.

The leafy shoots correspond closely in all respects with those of *Calamocladus grandis* (Sternb.). Zeiller[3] in his " Flore fossile de Valenciennes " figures and describes specimens of this type, and also a cone in connection with a leafy shoot. The latter is very similar to the present specimen, but was rather longer. Zeiller's figure (Pl. LIX., Fig. 6) shows an entire cone precisely similar to mine, but in his drawing to show details (Fig. 6 A) he represents the bracts as free to the base. Owing to the difficulty of making out the structure in impressions, I am inclined to think that this does not vitiate the conclusion that the cones described above are the same as *Calamostachys grandis*, Zeiller.

It may be useful to enumerate here the different species of *Calamostachys* which have been found as impressions in connection with the foliage of *Calamites* occurring in the British Coal Measures. (see Table on next page).

Calamostachys ludwigi, Weiss, belonged to foliage of the

[1] Weiss (84), p. 193, Pl. XXII., Fig. 9.
[2] No. 1057, Williamson Collection.
[3] Zeiller (86), p. 376, Pl. LIX., Figs. 4—7.

CONE.	LEAVES.

Paracalamostachys williamsoni,
    Weiss[1]
  = *Calamostachys grandis,*
            Zeiller[2]
	Calamocladus grandis,
	             (Sternberg)[2]

Calamostachys germanica, Weiss	*Calamocladus equisetiformis,* (Schloth.)[3]

Calamostachys sp.	*Calamocladus charæformis*
	    (Sternb.) [= *Asterophyllites*
	    roehli, (Stur)][4]

Calamostachys longifolia,
            (Sternb.)
	Calamocladus longifolius,
	    (Sternb.)[5] [? British.]

Stachannularia calathifera,
            Weiss
	Annularia sphenophylloides,
	    Zenk.[6]

Calamostachys tuberculata, Weiss	*Annularia stellata,* (Schloth.)[7]
Calamostachys ramosus, Weiss	*Annularia radiata,* Brongn.[8]

[1] Weiss (84), p. 193, Pl. XX., Fig. 9.
[2] Zeiller (86), p. 376, Pl. LIX., Figs. 4—7.
[3] Weiss (76), p. 47, Pl. XVI., Figs. 3 and 4.   Kidston (03), pp. 792, 807.
[4] Stur (85), p. 210, Pl. XIV., Figs. 13a, b, c.   Pl. XV.b, Fig. 3.
[5] Weiss (84), Pls. XX., Fig. 6.   X., Fig. 1.   XXI., Fig. 11.
[6] Weiss (76), p. 27, Pl. III., Fig. 11.
[7] Weiss (84), p. 178.   (76), p. 17.   Kidston (03), p. 809.
[8] Zeiller (86), Pl. LIX., Figs. 8 and 8A.   Weiss (84), p. 98, Pl. XX.,
    Figs. 1 and 2.

Calamocladus type[1], but its occurrence in Britain is uncertain. Kidston[2] thinks that possibly cones of this species have been included under the name of *Calamostachys typica,* Schimper, together with a *Palæostachya.* The foliage of *Stachannularia northumbriana* Kidst. is unknown, while the cones of *Calamocladus lycopodioides* (Zeiller) and *Annularia galioides,* Lind. and Hutt. do not seem to have yet been recognised.

    Hitherto, it has not been definitely known which impressions correspond to the petrified species *Calamostachys binneyana.* Dr. Kidston[3] has already regarded *Paracalamostachys williamsoni* as identical with Binney's cones, though Weiss[4] states that it differs

[1] Weiss (84), Pl. XVIII., Fig. 2.
[2] Kidston (03), p. 794.
[3] Kidston (03), p. 794.
[4] Weiss (84), p. 193.

from *C. binneyana* in the size and the form of the parts.   The present work upholds Dr. Kidston's view.

It may be noticed, however, that the differences between several of the impression species are apparently not great, and it is also just possible that previously, more than one species of petrified cone has been included under the name of *C. binneyana*.   In examining the specimens of this cone in large collections such as Williamson's, it has been found that many of them differ in slight details, such as the shape of the cone and the construction of the bracts.   The axis also seems to present many variations, but these may be wholly dependent on the plane in which the section is cut.   Again, apart from heterospory the differences between *C. binneyana* and *C. casheana*, are but slight.   Perhaps then, a closer study of the details of the cones, and the discovery of more specimens in continuity with leaves like the one described here, will show that the designation *Calamostachys binneyana* should be applied rather to a type of structure than to a species.   In view of this, it seems advisable to adopt for my cone a specific name founded on the foliage characters, viz., *Calamostachys grandis*.

Morphological Considerations.   The present specimen is of some interest in the discussion of the morphology of the cones of the Equisetales.

Summaries of the various views put forward as to the nature of the bracts and sporangiophores have been recently given by Professor Bower[1] and Lady Isabel Browne[2], and need not be repeated. Of the four current theories, the latter author adopts the view that the bracts of *Calamostachys* represent sterile lobes of the sporophylls, which have assumed their present structure and function by the loss of fertility.   I am quite unable to support this theory.   It has been shown above that the bracts are most probably foliar organs, and identical in structure, arrangement, and perhaps in number, with the leaves, though modified for their protective functions.   It seems quite unnecessary to look upon them as anything but leaves, and it is highly improbable that a sterilized sporophyll lobe should assume the exact structure and position of a leaf.

Though the present work bears on the nature of the bracts it throws little new light on the sporangiophores.   These may be (i.) fertile lobes of the sporophylls,   (ii.) cauline or axial structures, (iii.) organs *sui generis*.   There are difficulties in each of these theories.   In the case of the first, the numerical relations of the

[1] Bower (08), pp. 381—384.   [2] Lady Isabel Browne (09), pp. 2—21.

bracts and sporangiophores and their relative arrangement is an objection, for while the sporangiophores of successive whorls appear to be always superposed, the bracts of successive whorls alternate. Jeffrey[1] supposes a bifurcation of each bract to account for the usual case where the number of bracts is double that of the sporangiophores. The presence of the same number of segments in the leaf-whorls below the cone is perhaps an objection to this theory. On the other hand, Lignier[2] thinks the sporangiophores are of a double nature and represent two fused together. To both of these views, Bower[3] objects that the arrangement of the sterile and fertile whorls shows that they really have no relation to each other. When their arrangement is plotted on a plane surface this seems a real objection, but if a diagram is drawn, in which the successive whorls are represented as concentric circles, and a ground plan is obtained, the results are interesting. Assuming that each of the sporangiophores arises midway between the two bracts below it, it will be seen that very little shifting is needed to bring the former into their present position from what might have been an original alternating one. It is therefore scarcely safe, at present, to discard entirely the suggested connection between bracts and sporangiophores.

The presence in my cone of the whorl which I have called the "annulus" may be of some importance, but its structure is not yet sufficiently known to permit of any theory concerning it. It was probably considerably larger in the earlier stages of the cone, and may have primarily had some protective functions. Though its base appears leaf-like, yet its presence does not seem to disturb the alternation of the whorls above and below. It may possibly thus be homologous with the sporangiophores.

At the present time, I think that the evidence derived from the Equisetales is not conclusive in favour of any of the theories yet advanced as to the nature of the sporangiophores. Whatever may be the theory adopted, it ought to rest mainly on the data supplied by this group alone. Evidence supplied by other groups may be useful to confirm the conclusions reached, but it is scarcely safe, at present, to argue directly from species of one group to those of another.

[1] Jeffrey (99), p. 184—5.

[2] Lignier (03).

[3] Bower (08), p. 383.

SUMMARY.

1. A petrified cone closely resembling those previously described under the name of *Calamostachys binneyana* (Carr.), has been found for the first time attached to a leafy shoot. The leaves were small linear structures, arranged in whorls, and obviously Calamitean.

2. The structure and arrangement of the leaves and bracts is almost identical, but the leaves were not fused at the base The bracts appear to be, structurally, ordinary foliage leaves modified for protecting the sporangia, but they also had assimilatory functions.

3. Between the whorls of leaves a large number of small, black, hair-like structures occur on the stem.

4. At the base of the cone, below the last whorl of bracts, is a ring of tissue which seems to have considerable resemblance to the annulus of the cones of the modern *Equisetum.*

5. The cone described is probably identical with the impressions known as *Paracalamostachys williamsoni,* Weiss, and also with *Calamostachys grandis,* Zeiller, the leaves on the pedicel being of the *Calamocladus grandis* type.

6. Several species of *Calamostachys* have been found as impressions, attached to different Calamite leaves. Possibly the name *Calamostachys binneyana* applies rather to a type of structure than to a species.

7. This investigation furnishes part of the evidence required to finally settle the much discussed question of the affinities of *Calamostachys binneyana.* It also indicates that the bracts of the cone cannot be regarded as sterilised sporophyll lobes.

In conclusion, I should like to express my sincere thanks to Mr. Arber for his constant advice and assistance throughout my work.

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EXPLANATION OF THE PLATE.

Fig. 1.   Longitudinal section through the cone (Slide No. 1).   *ls.*, leaves at
the base; *a.*, "annulus"; *br.*, bracts. The section passes tangentially
through the whorls of leaves at the base.   × 4.

Fig. 2.   The same to show the "annulus" (*a*).   *b.*, bracts of lowest whorl;
ls., leaves; *h.*, hairs.   × 18.

Fig. 3.   Tangential section through the leaf whorls (Slide No. 1).   Leaves cut
transversely.   *a.*, near base; *b.*, near centre; *c.*, leaf cut longitudinally,
showing *s.*, sclerenchyma fibres; *m.*, "melasmatic tissue" of cells
with black contents; *p.*, pallisade tissue; *h.*, hairs.   × 25.

Fig. 4.   One of the cones with attached leafy shoot on slab in Sedgwick
Museum from Raven Shore.   × 3.   No. 449.   Carbon. Plant Coll.
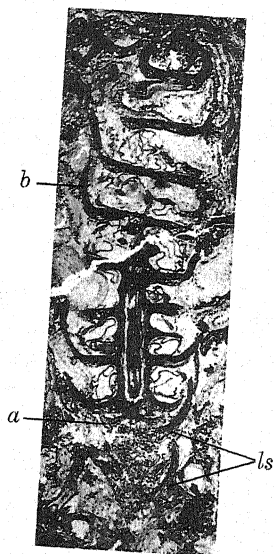
1
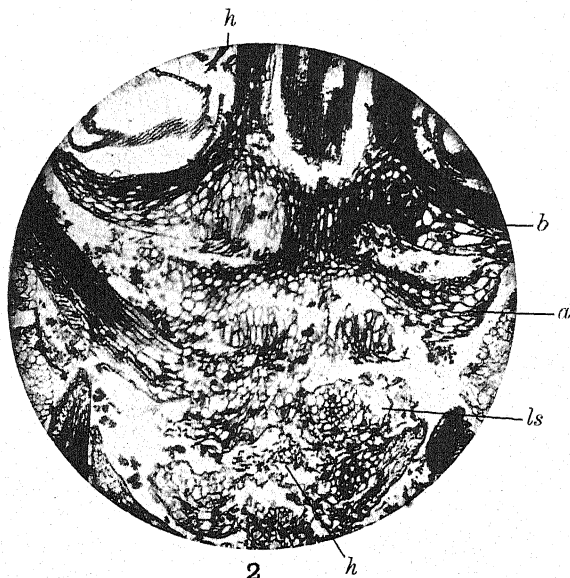
2
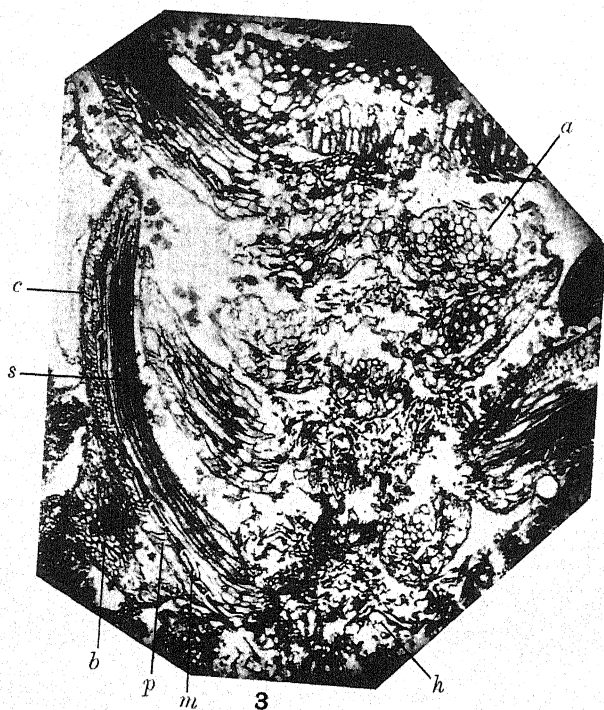
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H. HAMSHAW THOMAS.

CALAMOSTACHYS

THE DEVELOPMENT OF THE SPORES OF
EQUISETUM.

T HE structure and the development of the spores of *Equisetum* were very favourite subjects for study with the older botanists. Sachs, Sanio, Hofmeister, Russow, Tschistiakoff, and Leitgeb have all contributed to this subject, whilst of living botanists none has given us so valuable an account as Strasburger.

All are now agreed that the mature spore of *Equisetum* possesses four layers to its wall. On the extreme outside there is the spirally cleft wall which constitutes that curiously hygroscopic structure—the elater. Within this layer is a membrane which is usually spoken of as the "middle layer"; within this lies the "exospore,"[1] whilst the innermost and last-formed layer of all is the endospore.

When, however, we turn to the literature for information regarding the origin and interpretation of these four layers of the spore-coat we find a surprising diversity of opinion.

Without describing the opinions and labours of the different investigators in detail, I may briefly summarise the views which have been expressed regarding the development of the wall of these spores in the following manner :—

1. All four layers are formed by the spore-protoplast in centripetal succession.

2. The outer (forming the elater) and middle layers are derived from the special-mother-cell wall, the exospore and endospore from the spore-protoplast.

3. The outer layer is derived from the special-mother-cell wall, the middle layer, the exospore and the endospore are formed by the spore-protoplast

4. The outer layer is formed by the tapetal cytoplasm, the middle layer, the exospore and the endospore are formed by the spore-protoplast.

I have recently re-examined the development of the spores of two species of *Equisetum* (*E. arvense* and *E. limosum*) with the principal object of attempting to decide which of the above accounts is the correct one.

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[1] According to the interpretation which is given to the "middle layer" the "exospore" mentioned above corresponds to the whole or only to a part of the true exospore. As will be seen below I regard it as the true exospore in its entirety.

After a careful study of my preparations I have come to the conclusion that none of them completely expresses the facts and in the present note I will briefly state the results of my study of this and of a few other points in the development of these spores.

The spore-mother cells form a solid mass of tissue in which the individual cells are separated from one another by delicate walls giving the reactions of pectic bodies. The tapetal cells form a continuous layer round the sporogenous tissue. Very soon the spore-mother-cells begin to separate from one another by the apparent splitting of the delicate walls between them. This splitting of the membrane first becomes noticeable at the angles between several mother-cells. In the meanwhile the tapetal cells have lost their separate individuality and have become fused into a plasmodium. This tapetal plasmodium commences to penetrate into the interior of the sporangium, making its way between the separating spore-mother-cells. It may be noted that tapetal cytoplasm, free from nuclei, first advances into the interior of the sporangium, and that only after a short, but appreciable interval, the nuclei make their way along the cytoplasmic branches between the sporogenous cells. At about this stage the division of the spore-mother-cells takes place. I have been able to confirm Osterhout's account of the development of the spindle during the prophases of the first meiotic division in every particular. The chromosomes proved too numerous and crowded to enable me to count them with any exactitude. The formation of these bodies from the spirem can be followed with comparative ease and is particularly interesting in the light of present day cytological discussions regarding this subject. The spirem can be seen from an early stage to be double, being composed of two parallel parts which usually lie very closely indeed together. This two-fold character of the spirem, although often obscured by the intimate approximation of the two component parts, was, however, observed over and over again when the search was careful and thorough enough.

This double spirem segments into the bivalent chromosomes in such a manner that the two constituent chromosomes lie side by side parallel with one another.

Although a certain polarity of the spirem can be seen at one period during this division and the thread is then thrown into a number of loops, no evidence could be found that the sides of these loops become approximated or that they bear any direct relation to

the pairs of chromosomes which subsequently develop. I think there can be no doubt that the pairs of parallel chromosomes which can be quite clearly seen in the later stages of the prophase and during the metaphase are derived from the segmentation of a spirem which consists of two parallel halves.

The very important point, however, still remains to be determined, whether the two parallel halves of the spirem are derived from the splitting of an originally single thread or by the approximation of two separate and distinct threads.

In the light of what has been observed in other plants in which the chromosomes have been seen to originate from a double spirem, and from certain, as yet not very conclusive, indications in *Equisetum* itself, we may expect the latter alternative to prove the correct one, although it is a point which is exceedingly difficult to determine in the present instance.

So far as they go, therefore, my observations speak very decidedly against the origin of the chromosomes of this plant from the approximated sides of loops, and they agree much more nearly with the views of the Bonn and Louvain schools.

Another interesting feature which is very nicely shown in these nuclei is the fate of the chromosomes during the telophase of the division.

It will be recollected that until recently most cytologists believed that during the telophase of division the chromosomes became joined end to end, and that the filament which was thus formed became gradually thinner and longer and coiled in every direction through the nuclear-cavity. The coils anastomosed with one another so that finally the chromatic contents of the nucleus formed a reticulum.

Grégoire and his pupils have, however, shown that in several cases at any rate there is no such end-to-end arrangement of the chromosomes during the reconstruction of the daughter-nuclei, but that the chromosomes become united by lateral branches which are spun out between them, and that at the same time they become more and more vacuolated. The resting daughter-nucleus, therefore, possesses an alveolar-reticulate structure. The series of changes which the chromosomes undergo during the reconstruction of the daughter-nuclei in *Equisetum* are quite like those described by Grégoire. At the conclusion of the anaphases the chromosomes are seen to be very closely packed together. After the nuclear membrane is formed the chromosomes begin to separate from one

another, but at certain points their soft semi-fluid substance appears
to remain adherent, and branches or connecting arms are drawn out
between them at these spots. As the nuclear cavity enlarges and
the chromosomes become more and more widely separated from
one another, the branches between them become proportionally
longer, and gradually the substance of the chromosomes appears to
be lost in the series of reticulations which are in this manner spun
out.

From what has been said it will be seen that there is a complete
reconstruction of the daughter-nuclei at the conclusion of the first
meiotic division. The second division calls for no special notice in
this brief communication. It may be mentioned here that I can find
no evidence of the degeneration of sporogenous tissue sufficient to
possess any theoretical significance. It is true that in a few
sections one or perhaps two degenerating cells could occasionally
be found, but I am inclined to attribute their occurrence to
peculiarities in the penetration of the fixing agent, and I do not
consider that any importance can be attached to them[1]. At the
conclusion of the second meiotic division the spore-tetrads are
completely separated from one another and are enveloped in the
massive tapetal plasmodium.

The young spores (or pollen-grains) of the majority of plants
which have hitherto been examined are enclosed in temporary walls,
often of a mucilaginous nature, which the older botanists called
the " special-mother-cell wall," and which Strasburger has more
accurately and concisely named the " special-walls."

Although the plasma-membrane limiting the spores of *Equisetum*
often stains rather deeply, and to some extent simulates a cell-wall,
I have come to the conclusion, after a very careful examination of
my preparations, that no special-wall is developed in this plant.

This fact is of some interest because several other instances
occur in which a very massive tapetal plasmodium is associated with
the feeble development or entire absence of the special walls. The
Ophioglossaceæ furnish excellent examples of this relation between
the two structures. *Arum maculatum*, among pollen-bearing plants,
is another instance of the association of an exceptionally massive
tapetal plasmodium with comparatively feebly developed special-
walls. In those plants, on the other hand, in which a secretion-

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[1] I have seen nothing to compare with the extensive degeneration
of sporogenous tissue described by Professor Bower in
Equisetum. I will, however, discuss this matter more fully in a
future communication when illustrations will be given.

tapetum occurs, the special-wall is seldom found wanting and is usually well developed.

Lycopodium, Isoëtes and *Ipomœa* are all rather striking examples in which a secretion-tapetum is accompanied by massive special-walls.

I believe that the explanation of this relation is to be found in the necessity for providing protection for the young spores in those cases in which a secretion-tapetum exists. The soft mucilaginous special-walls, which usually form a more or less massive investment to the spore-elements in sporangia provided with secretion-tapeta, serve as a moist packing round and between the spores, shielding these bodies from mechanical shocks and jars, and, above all, protecting them from too great a loss of water. Moreover, whilst they carry out this protective function, the special-walls are sufficiently extensible to permit of the growth of the spore-protoplast, and they do not interfere with the passage of the nutrient materials required by the developing spores.

In those sporangia in which a tapetal-plasmodium is formed at an early stage in development, this protoplasmic investment protects the young spores from mechanical injuries and dessication sufficiently to render the additional formation of a massive special-wall unnecessary.

The young spores of the tetrad separate from one another and lie, still without any cell-wall round them, completely enveloped in the tapetal plasma.

After a short time a cell-wall is developed round the spore-protoplast, and later a delicate cell-membrane is seen to line the tapetal vacuole in which the young spore lies.

The future history of these walls shows that the membrane round the spore is the exospore, whilst the membrane formed by the tapetum is the "middle layer."

I differ from my predecessors, therefore, in ascribing the "middle layer" of these spore-walls to the secretory activity of the tapetal plasma. I can find absolutely no evidence to support the view that a superficial lamellum of the exospore is split off to form a "middle layer," or that this layer has any relation to the spore-protoplast. Neither can it be derived from the transformation of the special-walls, as some botanists have supposed, since this membrane does not occur in *Equisetum*. Following the subsequent history of these spore-walls we find that the tapetal activity produces another layer of formation wall which is formed on the outside of the "middle

layer" and which now separates this from the protoplasm of the tapetum. We can, with the greatest certainty, observe that this new layer becomes the elater of the mature spore. The final layer of the spore-coat to develop is the endospore, which is produced within the exospore by the spore-protoplast.

It will be seen, therefore, that the conclusion to be drawn from these observations is that the exospore and endospore are both products of the spore-protoplast, whilst the " middle layer " and the elater are successively formed by the tapetal cytoplasm.

In conclusion I may point out that the ripe spore contains a very considerable quantity of chlorophyll in its protoplast, and also that when these spores are heated with concentrated sulphuric acid on a cover-glass, very pretty siliceous skeletons are left behind.

I have given above a brief outline of some features in the development of these spores, but a fuller account with illustrations will be published later. These observations were greatly facilitated by a Government Grant. RUDOLF BEER, B.Sc., F.L.S.

REVIEW.

"Études sur la Fronde des Zygoptéridées ; par Paul Bertrand."
" Etc. Text, pp. 286 8vo.; Atlas, Plates 16, pp. 35, 4to.
Lille, 1909.

THIS is in many respects a remarkable book. Probably no anatomical question relating to fossil plants has ever been treated so fully before, nor has any one set of characters been so systematically and consistently utilized for theoretical purposes. The scope of the book is limited; it is concerned with the structure of the frond in a special family of Palæozoic Ferns, and is practically confined to the anatomy and ramification of the vascular strands in the petiole and rachis, with only occasional references to other tissues. Little is said about the structure of the stem, nor is any account taken of stem-characters in the author's classification and phylogenetic hypotheses. The frond is often the only part of the plant known, and so it is only upon this organ that a complete classification can be based; to this extent the necessities of the case may justify a treatment of the subject which is inevitably one-sided.

It is singular that throughout the book we have met with no reference to a lamina—a striking omission which may a parti

explanation in the probability that so many of the fronds in question were sporophylls, destitute of any assimilatory expansions.

The memoir is perhaps the best illustrated account of petrified plant-remains which has yet appeared. The atlas contains 16 photographic plates; it is no exaggeration to say that every one of the 114 figures is a perfect reproduction of the section illustrated, while the preservation of the specimens is usually excellent. A certain number of very useful diagrammatic figures will further be found in the text.

The value of Dr. Bertrand's book depends greatly on the accurate observation of complicated detail, which could not be adequately discussed without the aid of a number of figures. All that can be done here is to give a sketch of his methods and conclusions, with a few critical remarks.

The starting-point of the exposition is the anatomy of the frond of *Stauropteris oldhamia*, to which Part I. (pp. 15-70) is devoted. The abundance of the specimens renders this species particularly favourable for working out the mode of branching of the rachis. Readers of THE NEW PHYTOLOGIST will be familiar with the main facts from Mr. Tansley's second Lecture in his Course on the "Evolution of the Filicinean Vascular System"; generally, a reference to that lecture will be the best preparation for the study of Dr. Bertrand's book.

The elaborate account of *Stauropteris oldhamia* (with which the more ancient species, *S. burntislandica*, P. Bert., is compared) is exceedingly interesting. The author has investigated in detail the peculiar mode of branching, tracing the exact course of the four protoxylem-groups, which, as he first showed, are not peripheral, but immersed in the corners of the wood. Like so many of the Zygopterideæ, *Stauropteris* gives off two rows of branches on either side of its rachis, and this process is repeated, the successive planes of ramification being, in this case, parallel to one another. Every stage of branching is followed, up to the fine and simple ultimate branchlets which bear the sporangia. An interesting point is that concurrently with the main branching, small lateral strands are given off to supply the "aphlebiæ," filamentous tufts, which have their homologue in many Zygopterideæ and other fern-like plants of the Palæozoic.

The author's account of the histology of the rachis on the whole confirms previous observations; he finds evidence of circinate vernation in the young frond. The sporangia are shortly

described in Chap. VI.; the author attributes to the present reviewer the opinion that the simple sporangial structure shows *Stauropteris* to be a primitive member of the Zygoptrideæ: as a matter of fact he quite agrees with the author that the frond-characters indicate a highly differentiated and specialized plant.

In the second part the structure of the frond in *Ankyropteris* is described in full detail. Stenzel's sub-genus is raised by Dr. Bertrand to generic rank, but with different and more natural limits. The type taken is the well-known British form commonly referred to Renault's *A. bibractensis*, but here treated as a variety, under the name *westphaliensis*. The double-anchor shape of the foliar bundle is familiar. In the author's terminology the middle bar is called the "apolaire" (from the absence of protoxylem); the four incurved "flukes" of the anchor are the "antennes," each terminating in a "renflement récepteur," while the outer bands of small-celled xylem constitute the "filaments." The tracheæ (protoxylem) are placed internally at the four points of junction between the antennæ and the filament, but the question whether other protoxylem-groups may not be distributed along the inner side of the filament is left open.

In this genus only one series of branches is given off from each side of the rachis, but the branch-bundle is oriented at right angles to the main strand, and the second plane of branching is at right angles to the first. The mode of ramification of the frond in the Zygopterideæ generally appears to be materially different from that of ordinary leaves.

The complicated process of emission of the secondary bundles is, for the first time, fully worked out; the main point is that the continuity of the "filament" is never interrupted. The bundle of the branch is widely different from that of the main rachis; the author shows much ingenuity in interpreting the former in terms of the latter, but the difference remains. The secondary branches of the rachis were named *Rachiopteris inaequalis* by Williamson.

After some other fronds have been described, Chap. VI. gives a short sketch of the stems (or "stipes" as they are called by the Bertrand school) of *Ankyropteris*. The author regards *Zygopteris Grayi* (Williamson) as being probably the stem of *A. westphaliensis*, a view which scarcely seems likely to be correct, considering that *Z. Grayi* is a roof-nodule fossil, while *A. westphaliensis* belongs to the coal-seam; neither does the identity of structure in the foliar bundle appear sufficiently proved.

It is strange that in describing the stem of *Z. corrugata* the author makes no mention of the internal system of small tracheides, which was described and clearly figured by Williamson in 1877,[1] and has often been referred to since his time. This seems to be a curious example of our author's comparative indifference to stem-characters, while he is so minutely accurate in everything that concerns the frond.

Part III., on comparative anatomy and classification, begins with the well-known Burntisland fossil, Williamson's *Rachiopteris duplex*, now frequently referred to as *Zygopteris*, but placed by the author in a new genus, *Metaclepsydropsis*. There is here relatively little to add to the account given by Mr. Tansley, though of course the facts are now brought into line with Dr. Bertrand's general theory.

The Devonian fossil, *Clepsydropsis antiqua*, Unger, is of special interest, for it has the simplest petiolar structure in the group, and is hence regarded by the author as the starting-point for quite a number of lines of descent. The transverse section of the main foliar bundle is somewhat dumb-bell-shaped, with the protoxylem internal, lining an elliptical space near each end; a single series of branches is given off on either side of the rachis.

The leaf-bundle of *Asterochlæna* (here treated as a distinct genus) only differs from that of *Clepsydropsis* in its symmetry, the section being convex outwards, while the branches are directed towards the lower (posterior) face of the frond—a unique case, according to the author.

The following chapter deals with the two genera *Diplolabis* and *Zygopteris*; the latter genus is sadly shorn of its old array of species and reduced to the *Z. primaria* of Cotta, alone. It remains to be seen how far later authors will follow Dr. Bertrand in his new classification; it appears to be true, however, that *Z. primaria* is more nearly allied by its foliar structure to *Diplolabis* than to the other species formerly referred to *Zygopteris* itself.

Chapter III., of this Part, is devoted to the highly organized genus *Etapteris*, another new creation, of which the well-known *Z. Lacattei* of Renault may serve as a type. The English form of Renault's plant is made a new species under the name *Etapteris Scotti*. The genus is characterized, on the author's view, by the great development of the " pièces réceptrices " which form the bulk

[1] Organisation of Fossil Plants of the Coal-measures. Part VIII. Phil. Trans. Royal Soc., Vol. 167, Pt. I., p. 214 ; Plate 6, Figs. 13 and 14.

of the four vertical arms of the H-shaped bundle. A very curious point is the mode of emission of the branch-strands, which in this case form a double series on either side of the rachis. The two secondary bundles on each flank are separate at their origin, but coalesce after they become free, and finally separate again to supply the biseriate pinnæ.

In Chapter V. the systematic position of *Stauropteris* is very fully discussed; the author's careful examination of all the details of the frond-structure and judicious weighing of the various possible objections strongly confirm the opinion that this remarkable type finds its natural place as a member of the Zygopterideæ.

In Chapter VI. of this Part certain genera are introduced which have hitherto been regarded as standing apart from the family. *Gyropteris sinuosa*, Goeppert, a petiole from Falkenberg, of Lower Carboniferous or perhaps Devonian age, is interpreted as having a Zygopteridean structure, though the curved bundle bears no obvious resemblance to that of the main petiole in any accepted genus of the group, and may be more appropriately compared with the secondary strands of *Diplolabis* or *Metaclepsydropsis*.

A more surprising point is the inclusion of *Tubicaulis* in the Zygopterideæ. This genus, from its stem-structure, appears to fall naturally into the *Botryopteris*-group, and to be widely remote from the true Zygopterideæ. Dr. Bertrand, however, troubles little about the structure of the stem, and is able to make the simple, inversely curved foliar bundle fit into his Zygopterid scheme. He makes the genus the terminal member of the following phylogenetic series: *Clepsydropsis, Metaclepsydropsis, Diplolabis, Gyropteris, Tubicaulis*. Now, according to a note of Dr. Bertrand's, published in the Comptes Rendus for last year, *Clepsydropsis* is the petiole of which *Cladoxylon* is the stem. If this be so, we must suppose, on the author's view, that the highly complex, polystelic and secondarily thickened stem of *Cladoxylon* underwent reduction to the extreme simplicity shown by the undifferentiated protostele of *Tubicaulis*, a singularly bold hypothesis, for which an ingenious "reading" of the foliar bundle scarcely affords an adequate basis.

The author is of opinion that the *Tubicaulis Sutcliffii* described by Miss M. C. Stopes is the stem of *Anachoropteris rotundata*; he does not appear to have seen any preparations of Miss Stopes' fossil, or he would probably not have ventured on this identification.

The inclusion of *Gyropteris* and *Tubicaulis* in the Zygopterideæ is, in the reviewer's opinion, the most questionable point in the

book. On the other hand the problematic genus *Dineuron*, Renault, of which a new species from Burntisland has recently been described by Mr. Kidston, is clearly shown by the author's investigation to be allied to *Clepsydropsis* and *Metaclepsydropsis*.

Chapter VII. gives a detailed and extremely useful statement of the taxonomy of the whole group, now including, as here defined, 11 genera and 25 species. It is followed by a table (p. 225), indicating the probable affinities of the genera, and the supposed relations of the family to the Anachoropterideæ and the Botryopterideæ in the narrower sense.

The author discards the ordinal name Botryopterideæ in the wide sense in which it was used by Renault and has generally been adopted since ; he employs the name Inversicatenales (proposed by his father) to embrace the three families, Zygopterideæ, Anachoropterideæ and Botryopterideæ *(sensu stricto)*. The name is probably too technical to command general acceptance, for it is only in comparatively few cases that the foliar bundle actually shows an inverse curvature (*i.e.*, with the convexity inwards).

Part IV. discusses the affinities of the Zygopterideæ with other families, beginning with the groups included under the order Inversicatenales. The author states incidentally that the stem referred by Renault to *Anachoropteris Decaisnei* is really a specimen of *Ankyropteris scandens* (Stenzel), the association of the stem with an *Anachoropteris* petiole being accidental (p. 227). He regards the Anachoropterideæ as probably derived from a Zygopteroid type intermediate between *Clepsydropsis* and *Dineuron*, while the Botryopterideæ *(sens. strict.)* form a parallel series. As regards the latter family the author's views appear to be based too exclusively on the study of the late species *Botryopteris forensis ;* it is a pity that the older and simpler forms, *B. hirsuta* (Williamson) and *B. antiqua*, Kidston, were not also taken into account, for, as Mr. Kidston says : " There seems to be a tendency in the petiole trace to become more simple in form as traced back in geological time." [1] The hypothesis that *Botryopteris* was derived from the Zygopterideæ is, however, interesting and tenable, though far from being established.

The next chapter compares the frond-structure of the Zygopterideæ with that of recent Ferns, as interpreted by the Bertrands and M. Cornaille. The detailed comparison confirms the position

[1] Kidston. On a new species of *Dineuron* and of *Botryopteris* from Pettycur, Fife. Trans. Royal Soc., Edinburgh. Vol. XLVI., Part II., p. 364, 1908.

of the group among true Ferns; the derivation of the later Fern-families from Zygopterideæ is regarded as possible, but unproved (p. 255).

The chapter on the Origin of the Zygopterideæ is of great theoretical interest, for the author here develops an hypothesis (in general agreement with the views of Professor Potonié and Mr. Tansley) that the frond was primitively a branch of the axis, but has lost its original radial symmetry in becoming specialized for assimilatory functions. This idea is suggested, in the present connection, by the peculiar mode of branching of the Zygopteridean frond, which may be interpreted as a relic of primitive radial organisation. The theory is no doubt strengthened by the extensive observations of the author, showing how widespread are the peculiarities in question, but the reviewer is still inclined to suspect that these remarkable fronds were specialized rather than primitive organs.

In Chapter IV. the important question of the relation of the Zygopterideæ to the Cycadofilices is discussed, with special reference to the ancient type *Calamopitys Saturni.* The author comes to the conclusion that the two groups may be derived from a common source, *i.e.,* from a class of Vascular Cryptogams in which the leaf or frond had not yet acquired its fundamental characters of symmetry and ramification (p. 279). It will be seen that this latter hypothesis again involves the assumption that the mode of branching of the Zygopteridean frond is a primitive character.

It may be mentioned that the author fully recognises the analogy in the structure of the bundle between *Lyginodendron* or *Calamopitys* and the Cycads (p. 266), a point which has recently been disputed by Professor Chodat on the basis of the researches of the Bertrand school.

Dr. Bertrand's monograph is undoubtedly a most valuable contribution to the anatomical study of fossil plants. The somewhat narrow scope of his work is fully compensated for by the accuracy and completeness with which it is carried out; though one may not always be convinced of the validity of the author's interpretations, or of the security of his theoretical conclusions, his conscientious and acute investigations will have a permanent value, and will tend to raise further the standard of palæobotanical research. D.H.S.

RECENT ADVANCES IN THE STUDY OF HEREDITY

(A Course of Lectures, for the University of London, delivered in the

Summer Term, 1909).

By A. D. DARBISHIRE.

LECTURE IV.

THE NATURE OF THE ALLELOMORPHIC PAIR.

IF it could be shewn that all the characters of organisms were represented in the germ-cells by material units or factors, which were associated in pairs in such a way that one was dominant to the other when they met in conjugation; and that these units segregate in the formation of the germ-cells, it might well be claimed that the key to the problem of heredity had been found.

The phenomena presented by the inheritance of the characters of *Pisum* to which we have paid especial attention are in 'complete accord with the supposed state of affairs set forth in the preceding paragraph. The mode of inheritance of the characters of the cotyledons of *Pisum sativum* is in close accord with the theory that the two characters, round and wrinkled for instance, are represented in the germ-cells by separately heritable entities; and we may fairly regard it as demonstrated that, when they meet in fertilization, one of them is dominant to the other.

If all the attributes of organisms could be analysed into unit characters, such as round and wrinkled, and their Mendelian behaviour in inheritance demonstrated, there is no problem in

heredity the solution of which would be beyond our reach and no conceivable mating the exact result of which could not be predicted.

There are very few, I imagine, who are so sanguine as to make this high claim for Mendelian principles. At the other extreme, however, there are those who assert that the Mendelian phenomena are of an anomalous nature and that the Mendelian principles are of very limited application. It shall be our endeavour to determine approximately where between these two extremes the truth lies. And perhaps the most convenient way in which we may tackle this question will be to trace the changes which the conception of the allelomorphic pair has undergone since Mendel's papers were discovered. The earliest idea was that two characters were associated in a pair, of which the one happened to be the dominant and the other recessive; that the two characters were of equal value or weight—were homodynamous, if we may so express it; and that, beyond the fact that one happened to be dominant and the other recessive, and one—for instance—yellow and the other green, there was no intrinsic difference between them of such a kind as to give any *à priori* indication which could tell us, before they were crossed, which of them would be dominant and which recessive. The matter of dominance could only be determined *à posteriori* by the result of mating.

This conception has now given place to a theory of the allelomorphic pair, which seems to be in much closer accord with the true nature of the difference between the two characters which compose such a pair, but does not afford so sure an indication of the result of the meeting of the two characters in conjugation, as its enunciation would at first lead one to expect. It is however undoubtedly an advance. According to it the allelomorphic pair is not composed of a pair of homodynamous characters; but consists of the presence of a single character and the absence of it. The presence is dominant and the absence is recessive. In this conception of the allelomorphic pair there *is* an intrinsic difference between the two component units of a profoundly important kind ; and with this difference the question of dominance is intimately associated. This theory may and perhaps even ought to, appear, to the reader not already acquainted with it, to have far exceeded the limits of legitimate hypothesis spinning. We shall therefore proceed to the consideration of an experiment of the kind to which the origin of the new conception was due and which, to a large extent, proves its correctness. And for this purpose one of the

characters of *Pisum* supplies us with suitable, and easily obtainable, material.[1]

Unlike the characters which we have considered hitherto, and belong to a very early stage in the life-history of the plant, the characters to which I now refer are not manifested until the plant is ripe and dry. They belong to the seed-coat of the ripe seed. One of them is a rather beautiful brown mottling on a paler and brownish background; to be more precise, it consists of a network of anastomosing brown areas between the interstices of which the paler brownish background is seen. Peas with this type of coloration are called Maple or Partridge Peas; and a pennyworth from a corn-chandler furnishes ample material for starting an experiment with. Carter's " Grey Pea " belongs to this type; so also does the *Pisum arvense punctatum* offered by Messrs. Haage & Schmidt, of Erfurt.

Another of the types of coloration which the seed-coat of *Pisum* may exhibit, consists of a greyish background over which is distributed pretty evenly a very large number of minute dots of an intense purple. The size of the dots is not uniform, but the limits of its variation are not very widely separated : the dots sometimes tend to " run," as if the paper had been wet when they were put on. The " French Sugar Pea " offered by Messrs. Sutton, and the *Pisum Jomardii* of Messrs. Haage & Schmidt's catalogue afford good instances of this type of coloration. I mention these instances so that the reader may, if he wishes, carry out the experiment I am about to describe. It is perhaps hardly necessary to say that if he is engaged in teaching it is very desirable that this should be done. The labour and expense are trifling; and the results are almost indispensable to an adequate demonstration of the subject.

For the sake of brevity we will call the Maple character M ; and the purple spot character P. The result of crossing a Pea bearing the M character with one bearing the P character is a Pea whose seed-coats bear *both* these characters. At first this sounds very much as if the result of this mating were a blend ; and it is not impossible that a careless searcher after instances of exceptions

[1] It is interesting to note how closely the theory enunciated in this paragraph resembles De Vries' conception of the nature of the Mendelian pair of characters. To De Vries, likewise, only one character is concerned in a Mendelian pair : but, according to him, the two units are not occasioned by presence and absence of a single unit, but by patency and latency of such a unit. See *Mutationstheorie*, II., p. 643, etc.

to dominance might put it down as such without further enquiry. It is, however, nothing of the kind, as we shall shortly see.

But what is the explanation? The theory which naturally presented itself was that M and P are not allelomorphic to one another—but that each is the dominant member of a pair, the corresponding recessive member of which was the absence of that particular character. That is to say the two pairs are Maple and its absence; and Purple spot and its absence. We may conveniently denote the absence of M by m, and the absence of P by p. If this theory is true the possession by the hybrid of the two characters is no more an instance of a blend, than is the fact that the result of crossing a yellow wrinkled Pea with a green round one is a yellow round hybrid which, just as in the case we are now considering, derives one character (yellowness) from one parent and the other (roundness) from the other.

That this theory does approximate fairly closely to the truth is shown by the composition of F_2. For if the two pairs of characters (M-m and P-p) are inherited separately, and segregation occurs in the manner in which, as we have seen, the characters of the cotyledons were inherited, we should expect F_2 to have the following average composition :—

$$9\,AB \quad : \quad 3\,Ab \quad : \quad 3\,aB \quad 1\,ab$$

in which A is the dominant, and a the recessive member of one pair, and B the dominant and b the recessive member of another pair. That is to say, in this particular case we should expect F_2 to have the following average composition :—

$$9\,MP \quad : \quad 3\,Mp \quad : \quad 3\,mP \quad : \quad 1\,mp$$

The experiment has not been carried out on a scale sufficiently large to justify the statement that these proportions obtain. But these four types have been recognized, and occur in proportions which do not differ widely from expectation.

I well remember the excitement with which I opened the dry pods of the plants of this F_2 generation. Plants with seed-coats which bore both M and P were in the majority; plants with M only, or P only, occurred in smaller quantities than MP, though in equal numbers. I had examined many plants before I found one bearing the mp character; and as I had not a very large number of plants, and this character is only expected to occur once in every sixteen individuals I became afraid that I might not see one. But I did ultimately obtain two such plants. And well do I remember the interest with which I looked on these Peas, in which the two units

absence of Maple, and absence of Purple spot were associated in one individual. The actual colour of the seed-coat is a pale homogeneous grey, which becomes browner with age.

Now it might be imagined that the hypothesis put forward to account for this case, the so-called Presence and Absence hypothesis, had only been elaborated to explain one or two outstanding difficulties. This indeed may have been its origin ; but its fate has been very different, for, as stated at the beginning of the lecture, this conception has supplanted the original form of it.

COTYLEDON COLOUR.

Let us now therefore consider it in its application to the two pairs of characters of the cotyledons which we considered in the previous lecture. And let us deal with cotyledon colour first. Expressed in its simplest, and earliest form, the hypothesis as applied to this case is that the pair of characters is yellow and absence-of-yellow on a background of green, which, according to the hypothesis, is obscured by the yellow and can only be seen when the yellow factor is absent. This is really not much more than stating the case in other terms. In the case of the seed-coats one of the pair of characters might have been spoken of as Maple and brown, instead of Maple and absence-of-Maple ; for the seed-coat must be *some* colour, and the background which we see when the seed-coat is characterized by the recessive member of this pair is brownish. So that it may be said, that all that we are doing in applying the Presence and Absence hypothesis to cotyledon colour is to call the pair yellow and absence-of-yellow instead of yellow and green. And this is perfectly true. But there is a series of facts which have been observed by Mr. E. A. Bunyard which make it possible to base the application of this hypothesis to cotyledon colour on a more substantial foundation.

By the application of certain chemical and photo-chemical tests, this observer brought the following facts to light. It is, probably, common knowledge that all Peas whether yellow or green when ripe and dry, are green when unripe. Such unripe Peas contain two pigments, a green one which is chlorophyll, and a yellow one which is a pigment of the xanthophyll series, always found in association with chlorophyll in the green parts of plants.

The chlorophyll can be well seen in sections mounted in glycerine ; it gives the " hypochlorin reaction " with glacial acetic acid ; and an alcoholic extract gives the characteristic bands in

the red, blue and violet. The simultaneous presence of the two colouring matters in the unripe Pea may be demonstrated in the following way. Some unripe Peas are steeped in alcohol; a green extract is thus produced; but it only remains green if it is kept in the dark. If it is exposed to daylight or even to gaslight, it fades to yellow. And a spectroscopic examination of this yellow liquid shows that it contains the same pigment as the extract of ripe yellow Peas.

Both yellow and green Peas therefore start with both chlorophyll and xanthophyll; and the difference between them is that in the yellow the chlorophyll fades during ripening. The green chloroplasts in yellow Peas gradually lose their pigment, as the seeds ripen, and when it has disappeared altogether they are left in the cell as pale yellow globules. This is as far as the facts go. The hypothesis which these facts seem to warrant is that the pair of factors to which the colours of the cotyledons of *Pisum* are due are not "yellow" and "green" but some factor which effects the fading of the chlorophyll during ripening, and the absence of this factor; of which the former, which results in the production of a yellow Pea, is dominant, whilst the latter is recessive.

COTYLEDON SHAPE.

The application of this hypothesis to the pair of characters pertaining to the shape of the cotyledons seems destined to throw much light on the fundamental nature of the two factors involved, although the form in which, on the analogy of the foregoing case, it first presented itself seemed unreal and preposterous. For, on this analogy, we should have to conceive of the pair as consisting of the factor for roundness and the absence of this factor on a background of wrinkledness But we shall see that, the two characters, round and wrinkled, can be shewn to be due to the presence and absence, respectively, of a particular factor. Some clue as to the probable nature of this factor was afforded by the attempt to elucidate the causes to which the wrinkling of wrinkled seeds is due. All Peas, whether round or wrinkled when ripe, are round when unripe; they also, of course, contain much more water than the dry ones. It is, therefore, not unnatural to suspect that the wrinkling of the wrinkled Pea may be due to the fact that, starting with a mass similar to that of the unripe round Pea, it loses more water during the ripening process than the round one does. It is not convenient to measure this; but the same end
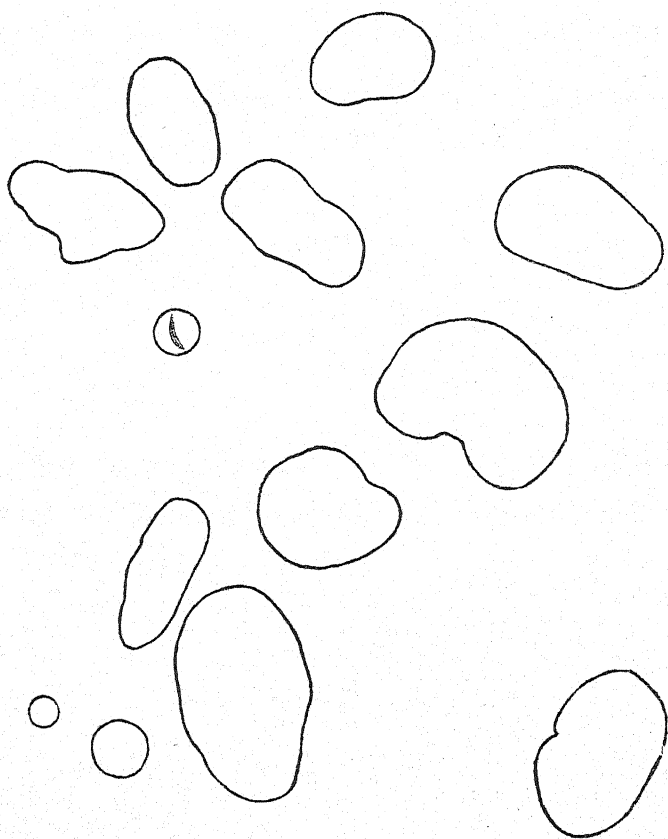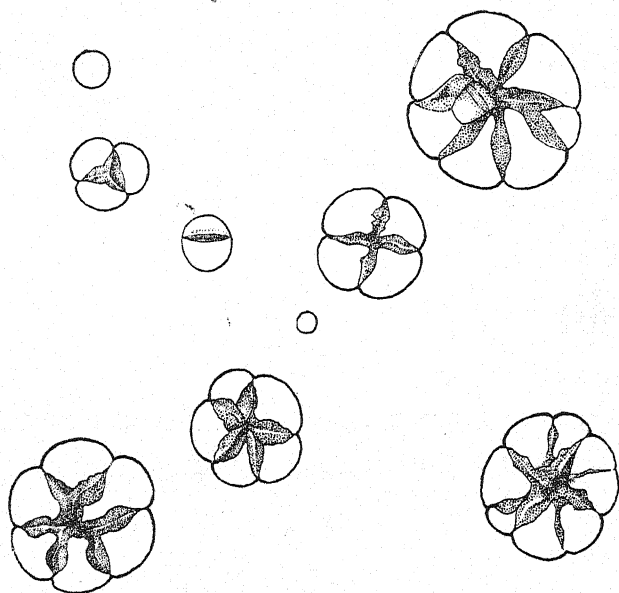
Fig. 1.—Starch Grains of a Round Pea.

Fig. 2.   Starch Grains of a Wrinkled Pea.

Note to Figs. 1 and 2. These figures have already appeared in Proc. Roy. Soc. B., Vol. 80, p. 122.   I take this opportunity for expressing my thanks to the Council of the Royal Society for permitting me to reproduce them here.

may be reached indirectly, by measuring the converse difference, namely that between the amount of water which a dry round Pea absorbs when it germinates and that absorbed by a dry wrinkled Pea under similar conditions. The result of such a determination is to show that a wrinkled Pea takes up very much more water in proportion to its weight when dry than a round one does. The method which I employed in this determination was to weigh the Pea dry, immerse it in tap water kept at as constant a temperature as possible and weigh it again after the lapse of twenty-four hours. The difference between the two weights of course gives the amount of water absorbed; and I propose to regard the ratio, expressed as a percentage, between this amount and the weight of the dry Pea as an index of the absorptive capacity of the Pea. Determined in this way the average absorptive capacity of some round Peas was 86%, and that of some wrinkled ones was 120%. It will be seen that whilst a round Pea does not absorb its own weight of water during twenty-four hours, a wrinkled one absorbs considerably more than its own weight of water. From this we are, I think, justified in concluding that the converse of the process which we have thus measured also takes place, namely that a wrinkled Pea gives up more water during ripening than a round one does.

Now, it is known that the reserve material in the cotyledons of *Pisum* first appears in the form of sugar, and that this is gradually converted into starch, which exists in the form of grains. It is further known that water can escape more easily from a sugary solution than it can from a starch grain; it is, so to speak, "locked up" more effectively in the latter than in the former. These two facts naturally lead one to suppose that the reason that more water escapes from the wrinkled Pea during ripening than from the round is that the water is only held by sugar in the case of the wrinkled and by starch in the case of the round. This is broadly speaking true: it is, however, not the case that there is no starch in the wrinkled Pea. But there are many facts which go to shew that there is a great deal more sugar in the wrinkled Pea than in round. In the first place the profound difference between the structure of the starch grains of the two types (see Figs. 1 and 2) suggests a fundamental difference between the chemical nature of the reserve materials of the two. In sections of the cotyledons the starch grains of wrinkled Peas can be seen to occupy considerably less space in the cells than the grains in round ones do: in the former there is no inconsiderable amount of interstitial material,

in the latter the cell is crammed with the starch-grains and there seems little room for anything else. And lastly the wrinkled Pea tastes distinctly sweeter than the round one, which in comparison has a very bitter taste. In connection with this last fact it is of no small interest to note that nearly all, if not actually all, of the improved Peas offered by Messrs. Sutton are wrinkled. What is the source of the sugar in the wrinkled Peas? It is presumably the remains of the sugar, in which form the reserve material was laid down, which has not been converted into starch. We are thus immediately led to the hypothesis that the pair of factors to which the shapes of the cotyledons of *Pisum* are due, are, not "round" and "wrinkled," but some factor which completes the conversion of sugar into starch and the absence of this factor. I say "*completes* the conversion" and not "*effects* the conversion" because *some* starch is formed in the wrinkled Pea: the difference between the two lies in the fact that some, but not all, of the sugar remains unconverted in the wrinkled Pea.

It has long seemed to me that of all the characters in animals and plants, the Mendelian inheritance of which has been demonstrated, this is the one the investigation of which seems to offer the surest prospect of describing the two units of a pair of characters in chemical terms. And I am at present engaged in the investigation of this material along these lines. There cannot be any doubt that such knowledge would be of the greatest scientific, and possibly of practical value. If the latter were to prove true it would be a curious, but satisfactory paradox that the re-investigation of a case, which might at first sight appear to be of purely historical and academic interest (the shape of the cotyledons being the first on Mendel's list of seven characters) should have such a result.

To return, however, to the Presence and Absence hypothesis: I propose now to consider one or two instances in which its application seems to be attended with greater difficulty than has been the case with those which we have already considered.

Under the heading, "Apparently parallel cases which are conflicting" (with the emphasis on the "Apparently" and not on the "parallel") let us consider the following paradox. *Urtica pilulifera* is the ordinary nettle with deeply serrated leaves. In *U. Dodartii* the bays are, so to speak, filled in; and the margin of the leaf is entire. The *pilulifera* character is dominant to the *Dodartii* character; *i.e.*, dissectedness is dominant to entirety. *Chelidonium majus* has a variety, *var. laciniatum*. But in this case the character

of *majus* is dominant to that of *laciniatum* ; *i.e.,* here entirety is dominant to dissectedness. In itself it is no explanation to say that it is obviously the normal which is dominant in the two cases, because if *Urtica pilulifera* were very rare and had been discovered after *U. Dodartii* it would be the variety, and *Dodartii* the normal But it is possible that the true explanation may underlie this one. It certainly is not probable that the two cases of dissectedness are manifestation of analogous germinal factors.

There are, however, further cases in which the result of the union of the two characters in a pair seems definitely to contradict the theory that the dominant member of the pair always consists in the presence of something and the recessive in its absence. In wheat the resistance to Rust, a disease caused by the attacks of *Puccinia glumarum* has been proved by Biffen to be a recessive character and susceptibility to be dominant. In resistant plants the growth of the rust-hyphæ is checked after they have entered the stomata ; and it is probable that the resistance is due to an anti-toxin. So that the *presence* of the anti-toxin is the recessive character and its absence is the dominant. To make the theory fit this case we we have to suppose that the dominant factor is one which prevents the formation of the anti-toxin.

Again the absence of glands on the leaves in *Matthiola incana* is dominant to their presence in *M. sinuata*.

But the fact that the theory meets with difficulties in its application to these cases should, so far from giving cause for misgivings as to its truth, tend to set us at ease on this score. If *all* the facts are consistent with a theory, we may be pretty sure that it does not even contain the germ of truth. No theory can touch (or be in contact with) all the facts ; so that if a theory touches some, it cannot touch others, and there will be hitches and difficulties somewhere. If there are to be no hitches, the theory must touch none of the facts. Instances of such theories suggest themselves readily to the mind.

DEVELOPMENT OF THE CLIMBING HABIT IN

ANTIRRHINUM MAJUS,

By T. W. Woodhead, Ph.D., F.L.S.

AND

Mabel M. Brierley.

[Plates II., III. and IV. and Text-Figs. 33—37.

IN recent years considerable interest has been taken in, and much attention paid to, the apparently sudden appearances of new characters in plants and animals. The work of Bateson and De Vries and of the school of energetic pupils that is growing up around them, has done much to bring these curious occurrences into line and also to give a steadily growing solidarity to the theory of mutation and to emphasise the importance of the discontinuity of variation.

Many of these so-called sports, though seemingly trivial in themselves, have their place in the scheme of evolution and a study of them is gradually helping towards a better elucidation of the origin of species.

It is with a view to adding a small contribution to this question, that the present study, which is but a preliminary to more extended work, has been undertaken, and deals with the appearance of an intermittent variation of a somewhat pronounced type. We have tried to avoid any temptation to push the facts beyond their legitimate limits and have been content, in the main, to place on record the facts observed, which we hope are of more than passing interest.

The illustrations, only a few of many which might have been given, will serve to show how prevalent, as well as how remarkable are the variations we have to describe.

That *Antirrhinum majus* does occasionally develop the twining habit has been frequently observed. Schenck[1] records climbing specimens and gives a figure (Pl. I., fig. 8); Pfeffer[2] refers to "certain European species of this genus" as being "inefficient branch climbers"; and Professor F. W. Oliver informs us that he observed climbing specimens in Kew Gardens in the early nineties, while

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[1] H. Schenck. Biol. der Lianen, 1892. I. Theil. pp. 177-8 and Pl. I., fig. 8.

[2] W. Pfeffer. Physiology of Plants. Engl. Transl., 1906, Vol. III., p. 45.

shortly afterwards they turned up in the garden of the late Mrs. Hubbard, also at Kew. One of these specimens, Professor Oliver has had preserved since 1894. In the later nineties this form turned up again in his garden at The Vale, Chelsea, in a batch of seedlings, but he was unable to winter it. In a letter from Dr. A. B. Rendle we learn that a specimen was sent to the British Museum in September last, which was found by Mr. J. Reeves of Wolverhampton.

The specimens which provided the material for the present study were noticed by Mr H. G. Brierley in his garden at Grimscar, Huddersfield, in the summer of 1908.

Each season Antirrhinums were propagated from cuttings and it was an invariable custom to plant cuttings of the white variety along a border in front of the house. The other colours were distributed in other beds in various parts of the garden.

For three or four years it has been the practice to sow Shirley Poppies behind the Antirrhinums. This bed, 4-ft. wide, presents a crowded appearance towards the end of the summer, and the usual admixture of these two species is shown in the photograph (Pl. II. Fig. 1), which was taken on September 21st, 1909. This border is in an open sunny situation facing S.S.W., and thus is exposed to the prevailing winds.

In the spring of 1908, prior to planting out the cuttings, the bed received a fairly heavy dressing of quicklime. The season was remarkable for its high winds and the plants were considerably blown, not only frequently, but for considerable periods, during which time the Snapdragons and Shirley Poppies were growing rankly together. The position of the border is such that it is passed frequently every day by those entering or leaving the house, but nothing peculiar was observed until September 24th, 1908, when during weeding operations, Mr. Brierley noticed that numerous branches of the Snapdragons had twisted themselves around the rough hairy stems of the Shirley Poppies, which were growing in close proximity to them. Many of the lateral branches had also twined around leaves and branches of the same or neighbouring Snapdragon plants. The appearance presented was that of a tangle of interlocked branches, and seemed so out of place in the Snapdragon that when our attention was drawn to it we decided to make a more careful and detailed examination of this interesting phenomenon. It was then found that this peculiar modification was developed in the white variety to a very remarkable degree.

A portion of one of these plants is shown in Text-fig. 33. In this case two slender branches have coiled around a rough flower stalk of the Shirley Poppy, whilst another one above has twined tightly around the flower stalk of the Antirrhinum. In two cases the leaves have been removed so as to show these branches more clearly.

Text fig. 33. Portion of Antirrhinum plant showing tendril-like branches, some of which have twined around the flower stalk of a Shirley Poppy.

To the left of the figure is shown a slender wavy branch, which was a common occurrence. Nor was the development of this habit an isolated case, for a careful examination showed it to be present in upwards of thirty individuals and it appeared to be confined to the white variety; the other varieties showing no trace of twining although growing under similar conditions. One point of difference however in their environment may be mentioned, that the plants showing the twining habit, growing, as stated above, in a border, 4-feet wide, in front of the house, were first caught by the wind in front, and then as the wind rebounded from the wall of the

house they were caught again from the opposite side and swayed
with a somewhat whirling movement against each other and the
Shirley Poppies among which they were growing.   Can it be that
we have here a stimulus which induced the branches to twine round
others for support ? or can it be that the previous period was one
which Weismann would regard as a period of constancy and that
now has come the period of changefulness ?   We believed we had
caught this Snapdragon in a " changeful mood " as Thompson puts
it, and we decided to humour it.   Meanwhile the plants were
examined and typical examples collected and preserved.   On
examination of these it was seen that while the main axis showed
no signs of climbing, tendrils were common on the lateral
branches, while a feature of further interest was that the coils they
formed were very variable, both in form, direction, and position on
the branch.   Text-fig. 34, A—E, show some of these found on the
specimens in 1908, from which it would appear that while
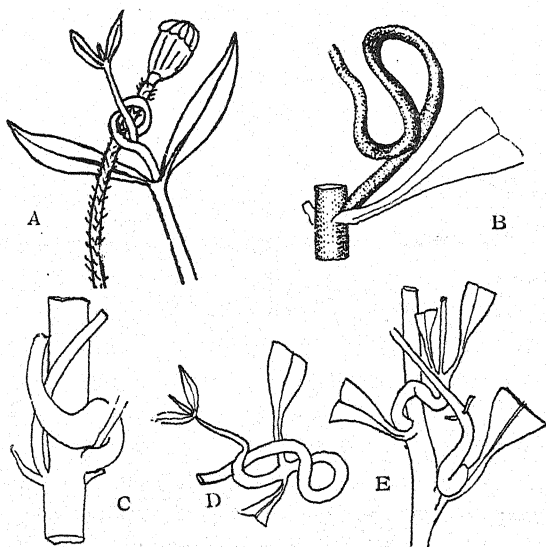
Text-fig. 34.   Climbing branches of Antirrhinum showing some of the
different positions on the branches where twining occurs.

the plant had shown this strong tendency to produce branch
tendrils it had by no means hit upon a single or definite method,
the only constant feature being that the tendency appeared only
in the secondary or later orders of branches.   It showed no signs of
twining in its main stem, unless the tendency to coil in the flowering
portion of the axis, to be mentioned later, belongs to this category.

In a few cases the older plants were too weak to maintain an erect position and resembled in habit the ascending stems of the Mint.

In Text-fig. 34, A, the upper internode of a branch has made two complete, though somewhat irregular, dextrorse turns around the flower stalk of a Poppy and then continued an erect course.

On the other hand in the specimen shown in Text-fig. 34, B, the coil has been developed in the lowest internode; this has made a nearly complete sinistrorse turn around one of the branches of the same Antirrhinum plant, not shown in the figure, then turned back in the opposite direction, but not in the same plane.

In Text-fig. 34, C, a coil is strongly developed in the first internode, but quite near the base, where it has made a nearly complete sinistrorse turn around a slender Antirrhinum branch, then suddenly reverses its direction like the one in Fig. 34, C, and continues obliquely across the stem, around which it forms part of a loose coil. On the way it crosses the opposite branch which in its turn has curved steeply around the stem to the opposite side.

In Text-fig. 34, E, are shown twining branches from the upper part of the stem where the leaves are alternate. The branches arising in the axils of the leaves at these two nodes have behaved in a manner similar to those in Text-fig. 34, C ; in each case, after making a basal coil in the first internode, the rest of the shoot crosses over to the opposite side of the stem.

The branch shown in Text-fig. 34, D, has twisted in such a way as to form a figure 8. Although such branches not uncommonly clasp adjacent stems or leaves, they more frequently develop these coils quite independently and clasp no support whatever, so that we cannot attribute the twining habit to the stimulus produced by contact with an adjacent branch.

In October, 1908, sixty cuttings were taken from this white variety of Antirrhinum and planted as usual in a cold frame and labelled. On May 13th of this year (1909) forty of these were planted out in the border above mentioned. The plants were small (4—6 inches high) and had not as yet developed lateral branches. These were kept under observation and by June 13th, lateral branches had freely developed, and of the forty plants in the border, twenty-five on this date showed signs of twining. In one case, both branches arising in the axils of a pair of opposite leaves, had each made a complete tight coil around the base of its subtending leaf, one of these passed twice around the stalk of its subtending leaf, clasping it closely in a double coil. Both these branches

twined around the petioles in a direction opposite to that shown in Text-fig. 35, A.

These branches did not develop further, but remained in this condition, their growing tips not elongating up to September 28th. The majority of the branches, however, had only made one third
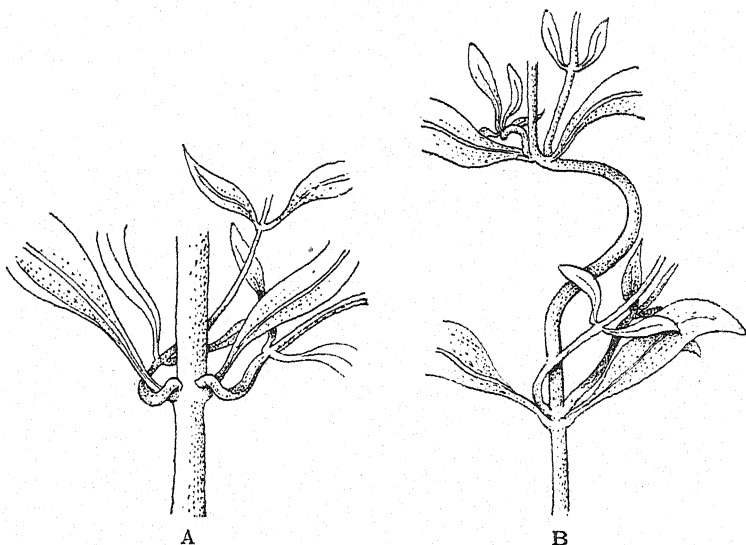
Text-fig. 35. A. Two branches at a node, each coiling around the base of its subtending leaf, but one sinistrorse, the other dextrorse. B. Two branches at a node, twining in the same direction. The internode above, also the upper left-hand branch, have formed sickle-shaped bends.

to half a turn or in some cases even less. This tendency towards the arrest of growth of the branches which developed the twining habit was very common but by no means general. On comparing Fig. 34, C and E, with Fig. 35, A, it will be noticed that the branches in 1908 had formed a coil at the base of the internode, but unlike many of those of the present year, this coil did not include within it, the stalk of the subtending leaf. On June 14th, the plants were carefully examined and an attempt was made to determine the length of time occupied by a branch in completing a coil. Twenty specimens were marked at points where branches showed signs of twining. These were examined at frequent intervals and sketches made. Indicators were also attached to show the position of the branch at the commencement of the observations. A very considerable number of drawings and records were taken, but with somewhat disappointing results. In one case, for example, from 7.20 p.m. on June 15th to 10.0 a.m. on June 17th, the marked branch had turned

through an angle of 45°. At 8.30 p.m. on the same day the branch was raised 2°, and at 10.20 a.m. on June 26th it was raised 20°, in which position it remained. The branch had in fact lost its tendency to twine and continued afterwards its normal course. In another case a branch curved at its base in such a way as to carry the shoot through an angle of 30°, from 7.45 p.m. to 10.20 a.m. the following morning. During the day, which was fairly bright, the upper part of the shoot erected itself and grew on in a normal direction, leaving only a slight curve at the base which became fixed. In a third case a branch shewing a faint trace of bending was marked on June 15th. By June 22nd it had made half a turn and by July 4th the coil was completed. The shoot made a complete dextrorse turn around the petiole of its subtending leaf. Meanwhile, a number of branches which had not been marked, completed their coils in a shorter period. It seemed curious that we were so unsuccessful in selecting favourable branches: still this is not surprising when we remember that a considerable number of branches, after curving to a slight extent, assumed a more or less normal position and continued their growth without further variation. It was also noticed that on dull days the coiling was more steady and continuous than on bright days.

It frequently happened that the curve produced during a dull period was more or less neutralised during a bright period. The twining branches noted up to this stage, *i.e.*, the end of June and early in July, had developed during a comparatively calm period. There was an absence of high winds, and the Shirley Poppies (sown behind them in the same border) had not as yet made their appearance. What was thought might be another contributory cause of twining was overcrowding, but up to this time the plants were too far apart to admit of this explanation. It was not until much later that the lateral branches had grown sufficiently to come into contact with each other, so that high winds, friction due to rubbing against their own or the rougher Poppy stems, or over-crowding, could not be seriously considered as contributory causes in this season's plants. As might be expected, when the plants were more fully developed and more numerous branches formed, a much larger number of twining shoots was observed. That this was during the period of overcrowding may fairly be put down as a coincidence and not a cause.

As seen above, from May 13th to June 13th twenty-five out of the forty plants had developed twining branches, by June 30th

thirty-three were noted and by the middle of July every plant in the border exhibited traces of it. Among these, all the various forms were noted which we found during the previous season, as shown in Fig. 34, A—E, together with several other variations.

A characteristic plant of this season's growth showed a tangle of coiled branches, many of which had twined around stems, branches or leaves of the same plant or around those of the Shirley Poppy.

Pl. II., Fig. 2 shows on a larger scale a Poppy stem caught in the strong coil of an Antirrhinum branch. On Pl. III., Fig. 1 two shoots of an Antirrhinum plant are shown; that on the right firmly held in the coil of the branch tendril coming from the left and seen in the centre of the photograph. Below and a little to the left of that are seen two tendrils which have formed perfect coils. The two lowest branches on the left are equally interesting, the lower of these twines steeply round the one above, in a manner quite typical of a habitual dextrorse climber.

On another branch of the same plant were found three successive pairs of twining branches, *viz :*—at the second, third and fourth nodes. In each case the coil grips firmly the base of its subtending leaf. Those at the second and third nodes have turned to the same side of the stem, *i.e.*, towards the light. A somewhat similar case is shown in the Text-fig. 35, A, and is of very common occurrence. The right branch tends to form a sinistrorse spiral around the subtending leaf, while the left branch forms a dextrorse spiral around its subtending leaf. It was different, however, with the branches of the fourth node. Both right and left branches had twined in a sinistrorse direction. We thus see how variable the twining is and that the branches from two nodes on the same axis may turn in opposite directions. An early stage in the formation of such coils is seen in the Text-fig. 35, B, where the left branch is turning towards the observer, then across the stem to the right, while the right branch turns away from the observer. The internode above has formed a rigid sickle-shaped or hook-like bend, which is repeated in the left branch arising from the node above. Similar hooks, but smaller, are frequent and are pretty effective in clinging to a support.

Not uncommonly a twining branch hooks on to a support by one of its turns but continues to twine independently. The same thing happened in one of our experiments. A slender stick was placed alongside an Antirrhinum branch which slowly twined

around it and held it firmly.   The rest of the branch, however, did not twine around this support; instead, it continued to twine independently of it, and eventually formed a spiral of two dextrorse turns above the point of attachment.   A careful examination was made of this plant with the following result :—

1. Number of branches which turned out of leaf axil and grew obliquely across the main axis. Sometimes both branches of a node crossed to opposite sides of the stem   24

2. Number of wavy branches forming a more or less loose coil, some showing distinct signs of torsion   14

3. Number of branches which after forming half a turn became sharply reflexed   8

4. Number of branches forming tight coils clasping the base of the subtending leaf   8

5. Number of branches forming tendril-like coils ...   12

making a total of 66 branches on one plant showing the climbing habit.

Occasionally this tendency appeared in the petioles of the leaves.   In some of these the petiole curved in such a way as to sharply reflex the blade, in others it twisted so as to carry the blade across the stem to the opposite side; in each case secondary thickening fixed the leaf in the assumed position.

We thus see that from some doubtful cause these plants have developed a tendency to twine.   These variations were confined almost entirely to the white variety, but of two specimens of a coloured variety (pink striped with dark red) grown at the end of the same border as the white ones, one developed four twining branches and the other five.   None of the other coloured varieties in other parts of the garden exhibited a trace of it.

That cuttings taken from the twining variety should have in turn continued the climbing habit was to have been expected and that they have done so, and in an increased degree, we have already seen.   It was a matter of interest, however, to determine whether the next generation grown from seeds of this variety, would do the same.   To test this point, seeds collected from the climbing form last autumn, were sown in March this year.   They germinated freely and batches of seedlings were planted out in various situations. The majority of these, however, have grown slowly and produced few lateral branches of sufficient length to determine yet whether or not this habit will be perpetuated.   One batch of seedlings was planted in a frame in the garden at Doe Royd, Almondbury, some

four miles distant. A number of these were in time planted out in different positions in the garden, but owing to the check received in transplanting, together with the cold, unfavourable season, very few lateral branches of suitable length have developed and none of these plants have as yet flowered. A few left over in the frame, however, fared better, and one of these was well in flower during the latter part of September. A portion of this plant (the white flowered variety) is shown in the photograph, Pl. III., Fig. 2. Just below the centre of the photograph, one of the branches may be seen which has formed a perfect coil around the stem of an adjacent Antirrhinum plant, which it is gripping firmly.

HISTOLOGY OF A TWINING SHOOT.

Another question that remains to be considered is:—Do these twining branches which so closely resemble in form and behaviour those of typical twiners, show any of their histological characteristics? Twining branches after being hardened in alcohol were sectionised both by hand and microtome.

Pl. IV., Fig. 1 is a photo-micrograph of a transverse section of a coiled branch. We see at once the close resemblance of this to the section of a typical twiner, such for example as is figured by Darwin.[1] The lower part of the section is the concave side, the upper part the convex side of the coil.

The tissues on the concave side are seen to be more compact; both epidermal and cortical cells are smaller than those of the convex side, and modifications will also be noticed in the tissues of the stele.

A comparison of coiled and uncoiled stems shows the following differences in the dimensions of the tissues:—

	Diameter of Stem.	Diameter of Pith.	Width of Cortex, Convex side.	Width of Cortex, Concave side.
Coiled Stem ...	1·590 mm.	·705 mm.	·385 mm.	·190 mm.
Uncoiled Stem	1·695 mm.	·940 mm.	·255 mm.	·255 mm.

Thus in stems of about equal diameter the twining stem has:—
1. A smaller pith.
2. A denser and narrower stele.
3. Cortex on convex side, ·130 mm. broader than normal.
4. Cortex on concave side, ·065 mm. narrower than normal.

Thus the excess of radial thickening on the convex side is about double the radial compression on the concave side.

[1] C. Darwin. Movements and habits of climbing plants, 1875, p. 74.

Text-fig. 36, A, shows a portion of the epidermis of the concave side of the coil seen in surface view. To the left of the figure the cells are elongated and this form of cell is continued over the convex surface. To the right are seen the cells typical of the concave side and it will be noted that they have undergone further division by vertical walls, which, as shown by Sachs[1] and others, are easily distinguished from the original walls.
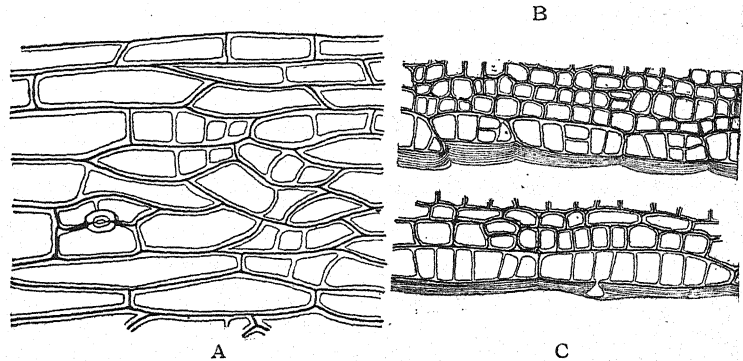
Text-fig. 36. A. Surface view of epidermis on concave side of coil showing secondary walls in the epidermal cells. B. L.S. epidermis and cortex of concave side, showing secondary division of the cells by both vertical and horizontal walls. C. Ditto with a pit in outer wall of epidermis.

Text-fig. 36, B, shows part of a longitudinal section, in which it will be seen that frequently further division has taken place in these epidermal cells parallel to the surface; this secondary division also occurs to some extent in the adjacent cortical tissues. In one instance a modified epidermal cell was noticed, in which a thin triangular pit occurred, as seen in Fig. 36, C, resembling the tactile pits, described by Haberlandt.[2]

The guard cells of the stomata on the concave side are level with, or slightly below the surface, and the air chambers are small, due perhaps to some extent to compression; while the guard cells of the stomata on the convex side are raised above the surface and the air chamber is larger. Modifications such as these occur only on the concave side.

As the season advances the differences between concave and convex sides become more strongly marked. Text-fig. 37, A, shows a portion of the outer tissues of an older coil on the concave side; here the epidermal cells are more strongly thickened, depressions are formed between the cells, and the cell-walls are often wrinkled

[1] J. von Sachs. Lectures on the Physiology of Plants, Engl. Transl., 1887, p. 95.
[2] G. Haberlandt. "Sinnesorgane im Pflanzenreich," 1901, p. 126.

as a result of increased compression, while the walls of the cortical cells have increased greatly in thickness and show well-marked pits in their walls.

Text-fig. 37, B, shows the thin walled outer tissues on the convex side of the same section.

In following these thickened elements round towards the convex side it was found that they disappeared first from the outer cortex and last in those cells adjacent to the endodermis.

A   B
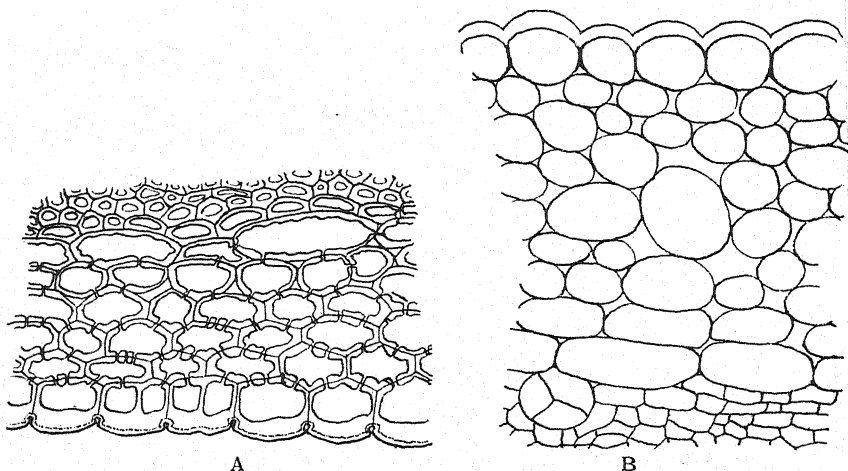
Text-fig. 37.   A.   T. S. of an older coil showing extent of thickening of cell walls in the outer tissues on the concave side.   B.   Convex side of same section as A, showing the thin walled tissues.

This thickening extends to the stele, and the pericycle becomes strongly sclerenchymatous, but only on the concave side.   Considerable increase also occurs in the vascular tissues.   This will be evident on comparing Figs. 2 and 3, Pl. IV. Fig. 2 shows the stelar tissues on the convex side, and Fig. 3 shows the stelar tissues on the concave side of the same section.   It will also be noticed in the latter figure that considerable secondary growth has taken place on the concave side, in strong contrast to its weak development or absence on the convex side.

The first perceptible change in structure is a slight difference in width of the cortex.   This appears as a flattening, probably due to loss of turgescence and consequent contraction of the cells on the concave side.   On this slightly flattened narrow side, the epidermis thickens, first on the outer wall, then on the inner, and finally on the lateral walls.   No trace of thickening in the cortex can as yet be seen.

In the pericycle, however, rather marked differences occur. Just within the endodermis one, sometimes two, small elements appear with distinctly thickened walls, these stand opposite to the phloem groups and are the first signs of pericyclic stereome while on the opposite (convex) side, there is no trace of them. In a fully coiled, mature branch these thickened elements have extended on the concave side to such an extent that they form a nearly continuous stereome band in the pericycle, whereas on the convex side no thickening whatever in this region occurs. In many cases, towards the end of the season, the coils had thickened considerably and a section through these thickened coils showed a very extensive development of xylem exactly similar to what occurs in many typical climbers. A complete cylinder of wood is developed and the coils become firm and rigid. This, which is part of the usual secondary thickening of the branch, becomes more pronounced in the region of the coil.

SUMMARY.

The twining habit appeared in a striking manner in many plants. While numerous branches of an individual were affected others showed no external signs of it. We have also seen that there is a refreshing absence of uniformity in the manner of twining as well as in the region in which the coil is produced.

Frequently twining takes place at the base of the shoot without reference to any object around which it could twine. In others the coil gripped tightly the base of its subtending leaf, modifications which are quite useless as a means of obtaining support. Still, may we not regard it as part of a variation in the race which in a modified form becomes useful ? In some, the coil at the base is a loose one, and may act as a hook and thus be useful for support, so also will be a more distant loose coil, especially during the swaying movements of the plants in a wind.

Other coils may be completed within a single internode. Or they may be formed by the upper part of one internode and the lower part of the next internode above, thus involving a node. And this may occur in any portion of the branch from base to apex.

Not uncommonly the flowering branches and the pedicels of the flowers show the same variation, but when flowering shoots developed the twining habit strongly, the flowers were usually aborted.

Again the coils may completely encircle a support in a close

or open spiral and thus possess all the advantages of a typical climber.

Still in spite of this well marked tendency to climb, the main stem is usually of normal strength and there is no evident need for the plant to develop the climbing habit.

If the original stimuli inducing the variation were put down to high winds and consequent extra friction, to overcrowding and to the extra dressing of quicklime, none of these would explain the behaviour of the second years' plants.   If we fall back on the supposition that these conditions of the habitat were contributory causes then their effect was very pronounced and so impressed on the plants, that the characters re-appeared, not only in the next season's plants grown from cuttings, but also in the next generation grown from seed.

The appearance of the climbing habit in Antirrhinum is of phylogenetic interest.   As Darwin[1] points out, four of the seven genera of the tribe Antirrhineæ, show climbing propensities, *viz :*— Linaria, Maurandia, Lophospermum and Rhodochiton.   These are chiefly petiole climbers, but *Lophospermum scandens* v. *purpureum* has sensitive internodes and *Maurandia semperflorens* has peduncles which exhibit feeble revolving movements and are slightly sensitive to touch.

In addition to these, and in the same tribe, *Antirrhinum Asarina* is a weak-stemmed trailing plant, and as noted by Schenck and others, the climbing habit appears in several other forms of Antirrhinum. In the case under consideration this tendency showed itself in a very marked degree.   We see, therefore, how strong the climbing tendency is within the tribe and it is of interest to find this habit asserting itself in non-climbing members of it.   That it has not been more strongly developed in the petioles is what might be expected in a short-stalked form like *A. majus* and the tendency has been transferred to the axillary branches, the basal portions of which are affected in a remarkable degree.   As we have seen many of the branches twine in a manner which, like the peduncles of Maurandia, cannot possibly be of service to the plant, but as Darwin says " by a little increase in power through natural selection they might easily have been rendered useful."   In this form of *Antirrhinum majus* it has gone a step further.   The family trait, from some unknown cause, asserts itself and many of the branches develop a tendril-like form of a very effective kind.

[1] Darwin, l.c., p. 66.

Finally an examination of the tissues of a twining branch shows all those histological modifications characteristic of climbing plants, in which the habit has long been hereditary.

We wish to express our thanks to Mr. H. G. Brierley for his kindness in taking the photographs of Fig. 2, Pl. II. and Fig. 1, Pl. III., and to Mr. S. L. Mosley for the drawings of Text-fig. 35, A and B.

Biological Laboratory,   *October, 1909.*
   Technical College,
    Huddersfield.

EXPLANATION OF PLATES

ILLUSTRATING THE PAPER BY DR. WOODHEAD AND MISS BRIERLEY

ON THE CLIMBING HABIT IN *ANTIRRHINUM MAJUS.*

Plate II., Fig. 1. The border of White Antirrhinums and Shirley Poppies in the garden at Grimscar, Huddersfield.

  Fig. 2. A thickened twining branch of Antirrhinum clasping a stem of Shirley Poppy.

Plate III. Fig. 1. Two twining shoots of Antirrhinum, the one on the right clasped in the centre by a branch from the specimen on the left. The lowest branch to the left has twined in a loose dextrorse spiral around the branch above; the next two higher branches show complete coils.

  Fig. 2. A portion of a plant grown at Doe Royd, Almondbury, from seed of the White twining variety, showing that the climbing habit appeared in the next generation.

Plate IV. Fig. 1. T. S. of a fairly young twining branch of Antirrhinum. × 25.

  Fig. 2. T. S. of vascular bundle of ditto on convex side of the coil. × 120.

  Fig. 3. T. S. of vascular bundle of ditto on concave side of the coil. × 120.

FIG. 1.

FIG. 2.

WOODHEAD AND BRIERLEY.—*CLIMBING ANTIRRHINUM.*
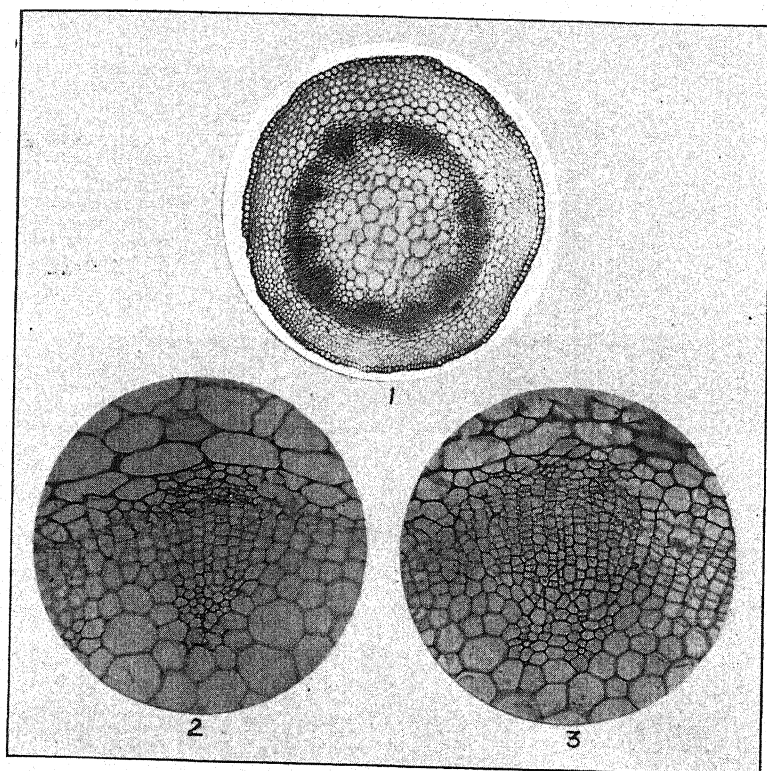
THE ANATOMY OF *MATONIA SARMENTOSA*, BAKER.

By R. H. Compton, B.A.,

Frank Smart Student of Gonville and Caius College, Cambridge.

[With Text-Figs. 38—43].

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THE genus Matonia was founded by Robert Brown in 1830 for the reception of the single species *M. pectinata* (Wallich, 13). The genus remained monotypic until 1887, when Mr. Charles Hose discovered in Sarawak a new species which was later described by Mr. J. G. Baker as *Matonia sarmentosa* (1, p. 256). In 1891, Baker figured a portion of the frond, sorus and indusium of the new species (2, p. 191 and pl. XIV.). Christ in 1897 gave a sketch of a portion of a pinna with his diagnosis (4, p. 337). The most complete description of external features, with notes on the morphology of the frond, is that of Diels (6, p. 343). In 1908 Copeland (5, p. 344) separated the species from the genus Matonia and placed it in a new genus Phanerosorus, " ob rhachin frondis sympodialem, pinnas dichotomas, et soros haud ad anastomoses venularium plurium impositos." While the habit of the frond is strikingly different from that of *M. pectinata*, it may be doubted whether the distinction is of generic importance. The two first characters mentioned by Copeland as distinctive are paralleled in *M. pectinata*. The rachis of *M. pectinata* is constructed on a sympodial pattern, according to Mr. Tansley and Miss Lulham, (11, p. 480) by the unequal development of the two branches of each successive dichotomy. The pinnæ of the young plants of *M. pectinata* are clearly dichotomous, and are of the ligulate form which is characteristic of the adult *M. sarmentosa*. As Tansley and Lulham remark (11, p. 481), " the resemblance of the dichotomously branched strap-shaped laminæ to those of the young *M. pectinata* is very striking." The character of the venation supplying the sorus appears to be sharply distinct in the two cases; in *M. pectinata* a reticulum of anastomosing veins underlies the sorus; in *M. sarmentosa* the sorus is supplied by a single vascular bundle. Professor Seward remarks (9, p. 192) that " as a rule comparisons based on venation characters and on the form of the frond are of secondary importance, and in some cases practically valueless; " and in this instance the differences between the fronds of the two ferns are seen to be super-

ficial, though the general aspect is strongly modified thereby. Further the resemblances between the two species in the structure of the sorus, the anatomy, histology, &c., are so remarkable that the separation of *M. sarmentosa* as a distinct genus seems hardly justifiable. The range of frond-form in many other genera is far greater, and the fundamental resemblances, so clear in Matonia, are often far more obscure, as for instance in the genus Trichomanes.

It is to the epiphytic habit that the peculiar form of *M. sarmentosa* must be related: the elongated pendent frond is apparently of the nature of an adaptation to the position in which the plant grows, and *Ophioglossum pendulum* may be quoted as a parallel.

The anatomy of *M. sarmentosa* has not been examined except for the observations of Tansley and Lulham on two fragments of rhizome. Both of these shewed a dicyclic arrangement, the inner cylinder in one case being haplostelic,[1] in the other solenostelic (11, p. 481).

The following results are based on material collected in Sarawak, and kindly sent by Mr. John Hewitt to Professor Seward, at whose suggestion the investigation was made.

Rhizome.

The rhizome of *M. sarmentosa* is an elongated creeping structure, averaging 3 mm. in diameter, thickly clad with long hairs, which, as in *M. pectinata*, have the appearance of being brushed upwards. These hairs consist of a single series of cells, which in the old rhizome have slightly thickened walls but still appear to have living contents (cf. Seward 9, p. 174): the transverse walls are mostly oblique.

On the dorsal surface of the rhizome are borne the scattered petioles: as in *M. pectinata* there seems to be no definite acropetal succession of fronds; young and old being irregularly placed, and in some cases abortion having occurred. On the lower surface are found the slender roots, which are inserted chiefly in the neighbourhood of the leaf-bases.

The rhizome forks here and there, and each branch appears to develope equally.

The epidermis consists of cells, spindle-shaped in surface view, the majority of which grow out into the ramenta, one hair being

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[1] The word haplostele is used throughout in accordance with Brebner's definition (see Ann. Bot. XVI., p. 523, 1902).

formed from each cell. The cortex is composed of elongated thick-walled cells with simple pits.

The endodermis is a thinner-walled single layer of cells with slight thickenings on the radial walls which break easily in cutting sections. Within this lies the single layer of thin-walled cells constituting the pericycle, which abuts directly on the proto-phloem.

The vascular tissues in the internode consist of two concentric cylinders, the outer being solenostelic and the inner haplostelic. The histology of the tissues is closely similar to that described by Seward for *M. pectinata* : the whole structure is, however, on a somewhat smaller scale. The crenulations of the solenostelic cylinder are not so marked as in the outer cylinder of *M. pectinata*, but more closely resemble those in the second cylinder in Seward's figure (9, pl. XVII., fig. 9). The general aspect of the transverse section of the internode is much like that of this figure if we imagine the outermost cylinder removed.

The xylem of the outer cylinder is encased as usual by phloem, proto-phloem, pericycle and endodermis, both within and without. The axial xylem-strand is surrounded by the other typical stelar tissues in the same way. Between the two cylinders lies a zone of sclerenchyma of the same character as that constituting the cortex, but of small and variable thickness, being usually broader on the ventral than on the dorsal side.

The sieve-tubes are of considerable diameter, and have rather thick walls which stain more intensely with methyl violet than do the tracheids. In this respect they differ from the sieve-tubes of the stem of *M. pectinata*, though in the petiole thick-walled sieve-tubes occur (cf. Seward, 9, pl. XIX., fig. 25).

BIFURCATION OF THE RHIZOME.

A series of sections was cut through the only bifurcation which was available, and the disposition of the tissues was observed to be as follows (Fig. 38) :—

Behind the fork there are present the two usual cylinders, lying quite free from one another. As we pass forwards to the fork the internal cylinder approaches the outer one and fuses with it by a broad junction in a dorso-lateral position. At the same time the outer hollow cylinder becomes elliptical in transverse section. The junction between the two cylinders then narrows

the elongation becomes more and more marked and constrictions appear in both outer and inner tracts of tissue. A strand separates first from the internal parts of the compound stele and lies free in the ground-tissue as an ordinary haplostelic strand. The constriction in the outer zone becomes more marked, and eventually
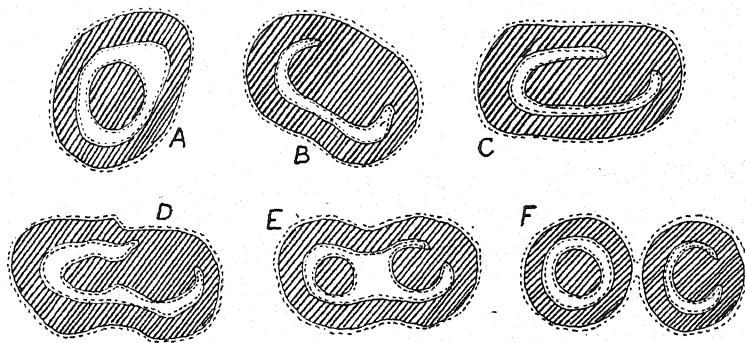
Fig. 38. Diagrams of a series of transverse sections through the bifurcation of the rhizome. Xylem shaded with lines. Endodermis a dotted line.

complete separation into two roughly equal portions takes place; the result being in the one branch a typical dicyclic structure; in the other a similar structure but with the two cylinders still united, later, however, becoming separate.

No ramular gap is produced in the process of branching.

Frond.

A transverse section of the petiole (Fig. 39) near its base shews a marked resemblance to that of the § Mertensia of Gleichenia (Poirault, 8, p. 176). The xylem consists of four groups of large tracheids united by bridges of smaller elements, the whole being arranged in the form of a distorted horse-shoe with incurved ends. The lumina of the large tracheids are often closed by accretions of a dark brown substance.

There are three protoxylem groups consisting of narrow scalariform elements, these being situated in the regions between the groups of large tracheids.

The centre of the petiolar bundle is occupied by a small strand of strongly thickened cells, of the same character as those of the cortical region. This is surrounded by an endodermis which is separate from the general endodermis of the bundle in this region. The internal and external pericycles are continuous with one another around the margins of the horse-shoe. The remainder of

the internal tissue is composed of parenchyma, but opposite each protoxylem there is a considerable mass of fibres with narrow lumina.

The protophloem, consisting of small angular elements, is almost continuous round the exterior of the bundle. The main sieve-tubes, however, are localised chiefly on the flanks of the bundle, and round the ends of the horse-shoe. They do not extend into the interior region, but whether they are here replaced by the above-mentioned fibres, or whether these latter are not true phloem structures could not be determined.
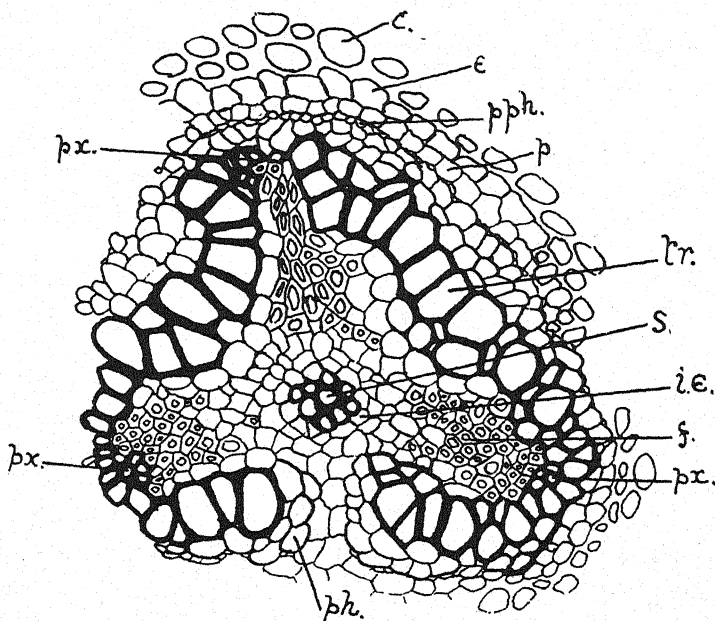
Fig. 39. Transverse section through a petiole near its base. *c.*, cortex; *e.*, endodermis; *p.*, pericycle; *pph.*, protophloem; *ph.*, sieve tubes; *tr.*, tracheids; *px.*, protoxylem; *f.*, fibres; *i.e.*, internal endodermis; *s.*, central sclerenchyma.

Further away from the base of the petiole changes take place in the vascular strand. The arms of the bundle separate somewhat, so that the internal parenchyma becomes continuous through the gap with the external tissues. At the same time the central group of sclerenchyma disappears. It forms a tough connection between the sclerised tissues of the rhizome and the base of the petiole, and no doubt functions mechanically as an additional resistance to the tearing-off of the frond at its base, where the greatest strain must fall.

As we pass along the petiole the bundle as a whole narrows somewhat by the disappearance of much of the central parenchyma. The xylem elements are reduced in number, but the brown fillings of the lumina, present in the base of the petiole, are absent further along.

The lamina presents no structural features of peculiar interest. It may, however, be noted that the curious projections of the walls in the lower epidermis present in *M. pectinata* (Seward, 9, p. 181) are also found in *M. sarmentosa*.

MORPHOLOGY OF THE FROND.

The complicated branch system of the frond may readily be related to a primitive type in which a series of dichotomies occurs:

Fig. 40. Diagram representing the mode of branching of the frond. The letters indicate the order of the branches to which they are affixed, the same number of dashes being given to each of the two branches arising by a single dichotomy.

such a type is represented by Dipteris, which is admitted to bear a close relationship to Matonia (cf. Bower, 3, p. 618). Professor Seward and Miss Dale (10, p. 508) consider the connection to be most evident with *M. pectinata* in respect of frond-character. In the latter species the inner branch of each successive dichotomy becomes a pinna, the outer forks again: the final result being a regular "scorpioid" branch system. In *M. sarmentosa*, on the other hand, the modification of the primitive Dipteris form of dichotomy has taken place in a different way, the final form of the frond being much less stereotyped than in *M. pectinata* (Fig. 40). The rachis forks repeatedly, and one of two things may happen:—
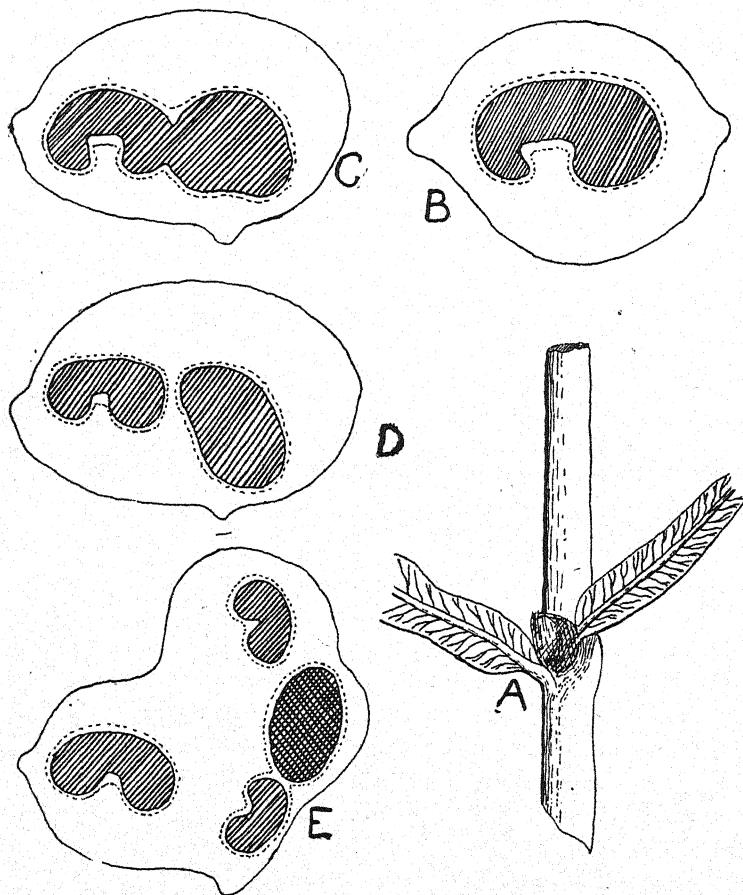
Fig. 41. A. Portion of rachis of frond, shewing an aborted bud and its two pinnæ. B,C,D,E. Diagrams of a series of transverse sections in the region of branching of the rachis. Xylem shaded with lines, endodermis a dotted line, epidermis a continuous line, aborted xylem cross-hatched.

(1) both branches may develop more or less equally, forming elongated axes which fork again and again: or (2) one of the branches may develop fully, while the other, after bearing a very few (usually two) pinnæ, ends in an aborted bud. This latter is the more usual process.

The dichotomous arrangement is preserved throughout. It is very distinct in the forked terminal pinnæ; and it seems probable that the appearance of pinnation in the frequent pairing of the pinnæ at the base of a rachis-segment is a secondary modification. This is borne out by a study of the manner in which the vascular bundles behave at the fork of the rachis (Fig. 41). The petiolar bundle divides in the median plane into two sub-similar portions. One of these passes directly into the sympodial continuation of the rachis. The other rotates through a right angle, and then gives off two successive traces, one of which goes to each of the two pinnæ, while the central strand disorganises completely in the aborted bud. Thus it is clear that the pinnæ are branches of the aborting rachis; and that they are produced by separate alternating dichotomies appears probable.

Tansley and Lulham (11, p. 478) inclined to the view that in *M. pectinata* the main fork of a frond is a dichotomy in whose angle a "middle lobe" is developed. This median pinna was compared with the bud in the fork of the frond of Gleichenia. They also mentioned the alternative view, namely that the "middle lobe" in *M. pectinata* is the inner branch of one of the dichotomies of the second order. This latter interpretation appears to fit in with the structure of *M. sarmentosa* better than does the former: for in this species there is nothing to correspond to the "middle lobe" (of the first theory), but the branching is a succession of subsequently modified dichotomies. The aborted bud, moreover, appears to be of different morphological value to that in *Gleichenia*.

Thus the comparison with the *Dipteris*-type appears more apt than with the *Gleichenia*-type: especially as the view which regards the latter as a modification of a pinnation appears the most natural (see Goebel, 7, p. 319 footnote), and as this view makes its connection with a primitive dichotomous frond more remote than is contemplated by Diels (6, p. 350) or by Tansley and Lulham (11, p. 479).

Root.

The stele of the root arises alone from the outer cylinder of the rhizome, without interrupting its continuity. At the base the

xylem appears to be triarch, this statement being all of which the material admits.

NODE.

Tansley (12, p. 196) remarks :— " The structure of the node (of *M. sarmentosa*) has not been examined, but there can be little doubt that the internal cylinder connects with the outer one either directly or by a branch." In the material which I have studied, and in which the central cylinder is haplostelic, the former alternative proves to be the true one. The arrangement of the vascular system at the node is of a simple type (Fig. 42), recalling the structure found in
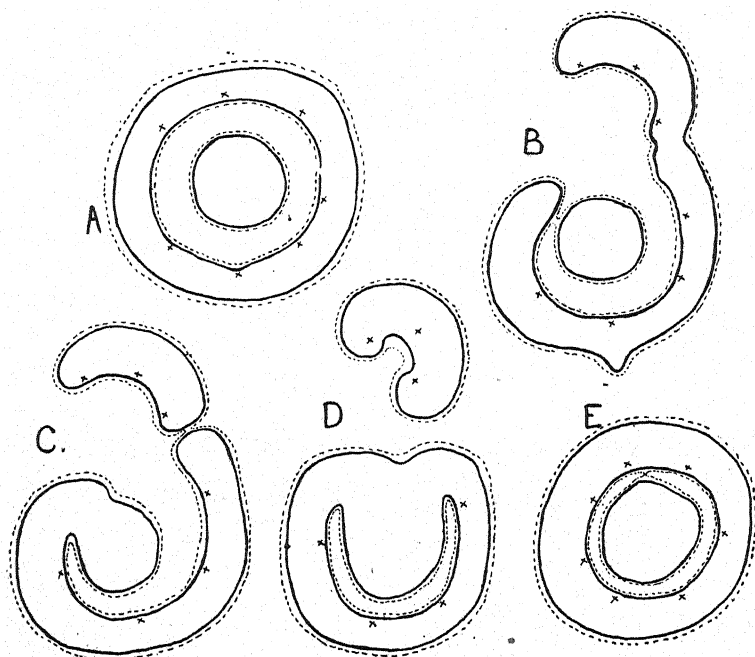
Fig. 42. Diagrams of a series of transverse sections through the rhizome at a node. Xylem outlined, protoxylems indicated by a cross, endodermis a dotted line.

immature plants of *M. pectinata* (Tansley and Lulham, 11, p. 498, E). An arc of vascular tissue detaches itself from the upper part of the solenostele, one edge becoming free before the other and the leaf-trace being tilted over to one side in consequence. When completely detached from the solenostele the leaf-trace is of the common gutter-shaped type, the comparison being rather with the leaf-traces of young plants of *M. pectinata* than with the adult. The leaf-trace consists of a xylem arc, completely invested in sheaths of phloem,

pericycle and endodermis, and carrying in its concavity a small strand of sclerenchyma, which, as above described, passes some little distance up the petiole and then disappears. The internal cylinder of the stem does not contribute to the leaf-trace directly, the complications due to the presence of inrolled margins in the leaf-trace of *M. pectinata* being absent in the species under consideration.

After the departure of the leaf-trace the haplostele approaches the margin of the gap in the solenostele from which the leaf-trace first became detached. A fusion takes place, the xylems of the two steles becoming continuous. Later on the other margin of the solenostele gap fuses with the axial strand, so that the internal ground-tissue is once more cut off from the exterior, remaining as a U-shaped strand in transverse section. The edges of the U
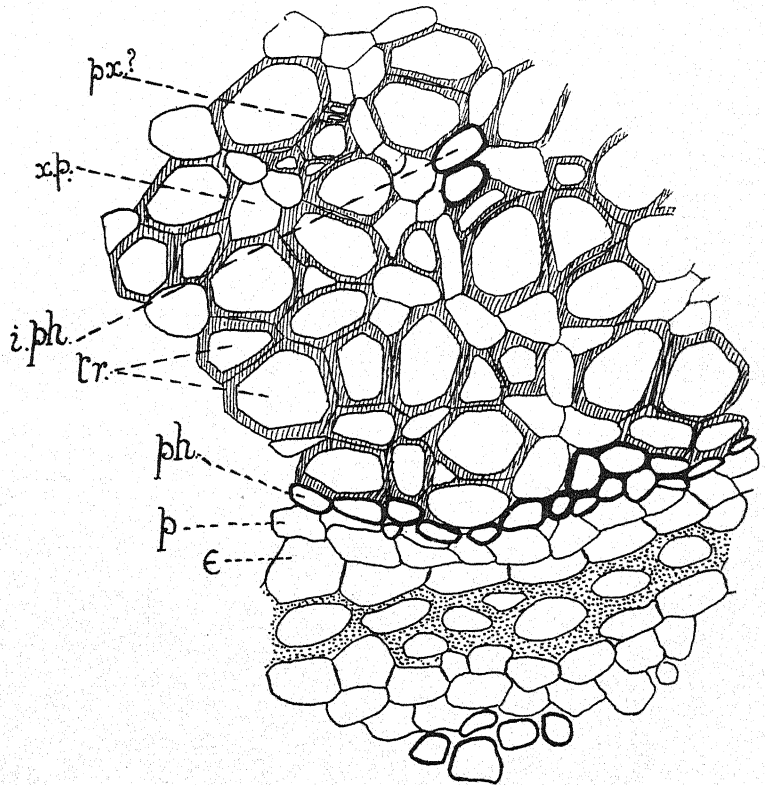
Fig. 43. T.S. of a portion of the central tissues of the rhizome in the region shewn in Fig. 5 D. *tr.*, tracheids; *px.*, protoxylem; *x.p.*, xylem parenchyma; *ph.*, phloem; *i.ph.*, internal sieve-tubes; *p.*, pericycle; *e.*, endodermis.

approximate and eventually meet, whereby the central vascular cylinder again becomes independent of the solenostele.

It is interesting to notice the occurrence of a definite "Lindsaya" structure[1] in connection with the node. In the region where the central cylinder fuses with the margin of the leaf-gap a very few (2—4) sieve-tubes appear in the centre of the axial stele (Fig. 6). As we pass forwards these sieve-tubes gradually approach one side of the xylem-cylinder, until eventually they unite with the general phloem of the exterior. The union occurs laterally, not at the dorsal point of fusion of the two cylinders, but at a point distant therefrom by about 90°.

PROTOXYLEM.

The protoxylems of the stem are by no means so distinct as those of the petiole, but in the solenostele there appear to be about seven groups of small scalariform tracheids, opposed to slight centrifugal projections of the layer of sieve-tubes, but not producing marked crenulations in the outline of the xylem ring. At the departure of the leaf-trace three dorsal protoxylems pass off, and presumably are continuous with the three protoxylems of the petiolar bundle; the actual connection, however, was not observed.

In the central cylinder a group of unusually small scalariform tracheids was observed in the region of fullest fusion with the solenostele (Fig. 43). It is suggested that this may represent a rudimentary protoxylem. It is to be noticed that it appears at the same point as do the internal sieve-tubes—that is, at the point where the transition from protostele through the Lindsaya-type, to solenostele is taking place.

In conclusion I wish to express my indebtedness to Professor Seward for placing the material at my disposal, and for valuable help in the work.

[1] See Tansley and Lulham, Ann. Bot., XVI., p. 157, 1902.

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REVIEW.

The Cultivation of the Fungi.

"Untersuchungen aus dem Gesammtgebiete der Mykologie, von Oscar Brefeld.   Band XIV, Die Kultur der Pilze, pp. VIII. + 256. Münster i. W., 1908."   Preis 16 Mk.

IN the present volume Professor Brefeld has collected together the chief results of his practical experiences in the various methods of tracing the life-history of the Fungi, a work which extends over a period of more than forty years.   We must remember that it is to Professor Brefeld that we owe the invention of the method, which dates from 1868, of starting fungus-cultures from a single spore, and until this method met with universal adoption, most of the accounts dealing with the life-histories of the various Fungi were unreliable.   The magnificent results achieved by Brefeld himself through consistently following his method of pure culture are contained in the first thirteen volumes of this work, which have appeared from time to time starting with 1872.

The first part of this volume deals mainly with the germination of the spores of Fungi, and with the methods employed for their further successful cultivation. It embraces also a very useful general account of the biology of the group. It is based on the axiom which we find frequently insisted on throughout the book, viz. "To carry out reliable investigations in Mycology, the first and most essential requisite is to start with pure spore-material, to prepare cultures from this containing only a single spore in a suitable transparent nutrient medium, which must be entirely free from all other spores, and to follow continuously the growth of the mycelium from the spore throughout every stage in its development avoiding any possibility of contamination from outside until we arrive again at the production of spores similar to those with which we started."

Discussing the germination of the spores, Brefeld points out that the extraordinary fertility of the Fungi is rendered possible through the minute size of the spores, involving a small expenditure of material in their production, and their lightness assists naturally in their dissemination by currents of air. They may be considered as the "plankton" or floating organisms of the atmosphere in a resting condition. When the air is still they gradually sink to the earth, where under favourable conditions they germinate.

As one result of the minute size of fungus spores the amount of stored-up food-material which they contain is usually very scanty, hence, in pure water either germination does not take place at all or only a very limited development is reached.

Exceptions to this general rule are to be found principally in those forms which possess comparatively large spores and so are better provided with a store of food-material, and also frequently in the Fungi which live as parasites and hence are dependent upon their own resources to provide the means for their germ-tubes to penetrate into the tissues of the host. The Peronosporineæ and Entomophthoraceæ furnish instances of the latter.

As examples of spores which are well provided with food-material, the chlamydospores, zoospores and oospores of the Phycomycetes and the teleutospores of the Uredineæ may be mentioned. Many of these, however, which are generally provided with a thick cell-wall will germinate only after they have passed through a resting-stage of longer or shorter duration.

To preserve spores of this kind, so as to maintain their vitality until the requisite period of rest has elapsed, Brefeld recommends, after obtaining the spores in as pure a condition as possible by repeated washing and centrifuging, that they should be mixed with white, sterilised, powdered glass and spread on the surface of clean, pure sand contained in a flower-pot and kept moist by the addition of sterilised water supplied from below. The powdered glass is to be covered with a layer of clean, well-washed, damp moss and the flower-pot should be kept in a cool place, sufficiently lighted. From time to time samples may be removed, the spores separated from the powdered glass and sown in water until germination is found to take place. Sclerotia which may require likewise a period of rest may be similarly treated.

With respect to the greater number of fungus-spores which will not germinate in pure water, these are as a rule adapted to live

on dead organic substances, from which under suitable conditions of moisture, etc., they obtain the nutriment essential both for their germination and for their further growth.

Brefeld shows the important part that herbivorous animals play in the dissemination of the spores of Fungi. The animals devour various parts of plants on which spores have fallen, the spores pass unharmed through the alimentary canal and are voided with the fœces, and these provide an extremely favourable medium for their germination and the subsequent growth of the Fungi resulting from them. In fact with some forms, especially in the case of those usually found growing on dung, the passage of the spores through the body of an animal seems essential before germination can take place. Spores of some coprophilous Fungi have however been induced to germinate artificially by sowing them in a decoction of dung maintained at a temperature of about 87° F., when neither condition by itself sufficed to bring about the required result.

Dung has been found to provide one of the most suitable media for cultivating Fungi and a decoction for this purpose is very easy to prepare. The decoction may be evaporated down to one-tenth of its bulk without deterioration and in this concentrated condition it is secure from decomposition by the entrance of chance fungus-spores. In this state it may be kept for almost any length of time, and may be transported for long distances, *e.g.*, to tropical regions where horse-dung is sometimes unprocurable, and when required for use may be restored to its original bulk by the addition of water.

The plan recommended of covering the mouths of flasks in which culture-media are kept with two thicknesses of filter-paper, the inner one sterilised with alcohol and the outer one with mercuric chloride is an improvement on the plugs of cotton-wool generally employed for this purpose, as less likely to lead to the introduction of particles of dust and other impurities when the flasks are opened to remove some of the contents.

A decoction of plums or other fruit for those fungus-spores which require an acid medium for their germination, and the well-known beer-wort are other useful culture-media and, like the dung-decoction, may be evaporated down to a small bulk and preserved in this state until they are required for use. Various mixtures of any or all of these may be employed. Meat-decoctions find their application in the cultivation of Bacteria and of the Fungi which attack insects, e.g., *Empusa, Entomophthora, Cordyceps, Laboulbenia*, etc., and those forms which live on horn-like substances.

For cultivating parasitic Fungi, the suitability of a nutrient medium prepared from those parts of the host on or in which the parasites usually live is obvious. Thus, Brefeld obtained an excellent growth of *Phytophthora infestans* with the production of conidia by using an extract prepared from potato tubers, and of *Nyctalis parasitica*, which in nature is always found growing on the cap-shaped fructifications of species of *Russula*, by the employment of a watery extract of the latter. Closely related to this is the observation that in nutrient solutions prepared from the fructifications of various Basidiomycetes, the spores of these and also of other Fungi germinate more readily than in other media.

One or other of these solutions will usually suffice to bring

about the immediate germination of most fungus-spores, except in the case of those which must pass through a preliminary resting-period. With certain Fungi, however, e.g., *Leotia*, *Geoglossum*, etc., among the Ascomycetes and Lycoperdon, *Geaster*, *Phallus*, etc., among the Basidiomycetes, all attempts to procure the germination of their spores have so far yielded negative results. It is possible that they require a longer resting-period before they will germinate than has yet been allowed to them.

The need of high temperatures approximating to those of warm-blooded animals to bring about the germination of the spores of coprophilous Fungi has already been mentioned. The reverse has been found to be the case in *Tilletia caries*, the spores of which germinate imperfectly or not at all at temperatures exceeding 20°C, while at lower temperatures, even down to 6°C, most of them will germinate.

The power of vegetative reproduction possessed by the fructifications of the Basidiomycetes is not generally known. Almost any part of the stipe or the young pileus of some forms, when placed in dung decoction, will produce a mycelium, in its turn bearing the fructifications. The conditions essential to bring about this are, that the pieces employed for this purpose must be carefully cut out and handled, that the nutrient solution employed must not be that too concentrated and, that the pieces must be only laid on the solution and not entirely submerged. This method of propagation affords manifest advantages in the case of those species of which the spores are difficult to germinate.

The methods previously considered deal principally with the employment of clear nutrient solutions to bring about the germination of the spores, or to start the growth of the Fungus in other ways. To follow the further growth of the germinated spores, especially with those forms in which the mature fructifications reach a considerable size, solid substrata have to be used. The substances recommended by Brefeld are chiefly those from which the nutrient solutions were prepared and of these lumps of fresh horse-dung take the first place. The lumps may be sterilised in glass-dishes provided with a cover, and in this condition can be kept for any length of time without giving off any perceptible odour. Plums soaked in water, or the dried fructifications of the larger Fungi steeped in water or in nutrient solutions, prove very suitable for the cultivation of certain species.

But the objection to these substances when employed in bulk is that they are not sufficiently porous, and insufficient access of air exercises an unfavourable influence on the growth of many Fungi. Two substances in which this disadvantage is absent are bread and sawdust. Fresh bread when well baked is practically sterile, but if the cultures are likely to be of some duration, slices cut with a sterile knife may be further sterilised by heating to a temperature of 50° to 60°C a few times at intervals of two or three days. This temperature must not be exceeded because the physical characters of the bread on which its value largely depends, are thereby altered. The slices of bread may be damped before sterilisation with any nutrient solution.

Many Fungi grown on this medium attain to a most luxuriant

growth such as is never found elsewhere in their free state. In fact, Brefeld suggests that in certain cases the development of a fungus may be carried a step further by artificial cultivation than can ever take place under natural conditions. An apparent instance of this is the production of the ascocarps of *Penicillium glaucum*, the special conditions for obtaining which by growing this mould on slices of bread are fully described. By taking the necessary steps, Brefeld never failed to obtain the ascocarps when he required them, but, so far as is known, they have never been met with in nature, in spite of the ubiquity of the fungus itself.

The sawdust of various woods furnishes another valuable culture medium when damped with a nutrient solution, largely on account of its porous nature, and is particularly suitable for those forms which grow principally upon wood. The usefulness of certain ripe fruits for the cultivation of Fungi is often overlooked. Bananas may be specially mentioned: after removal of the peel, the flesh which is not too rich in sugar and sufficiently porous in structure is obtained in a sterile condition and after leaving it for a short time to become soft, it forms a most favourable culture medium, especially for the Mucorineæ.

Brefeld, from his wide experience does not speak so favourably of the various nutrient media prepared with the addition of gelatine or agar-agar, which are so generally employed for cultivating Fungi. He admits that they have their special advantages, particularly in the cultivation of bacteria, also for obtaining pure cultures from a mixture of fungus-spores, for transporting living cultures of Fungi for long distances, for the biological analysis of air and water, etc., but Fungi grown on them never reach the same luxuriant growth as they do on other substances, more particularly on bread and sawdust.

We may now turn to the external conditions which can in certain cases exercise an influence, favourable or otherwise, on artificial cultures of Fungi and hence must be taken into consideration. In this connection, the well-known work of Klebs has already shown to how great an extent the phenomena of reproduction in the lower Fungi and Algæ may be influenced by external circumstances. Some further instances of this are contained in the present volume.

When Fungi are grown in nutrient liquids the degree of concentration is of importance. Thus, in very concentrated solutions, *Sporodinia grandis* produces zygospores only, while in dilute solutions the asexual sporangia alone are formed. It is found that many parasitic Fungi will grow only in very dilute nutrient solutions. When solid media are employed the amount of moisture they contain plays an important rôle. *Coprinus stercorarius* forms exclusively sclerotia when grown on a decidedly damp substratum, but on a drier substratum the cap-shaped fructifications are produced without the previous formation of sclerotia.

Nor can the influence of light be neglected; it has not been shown to be essential for the vegetative development of any fungus but without a sufficient intensity of light, a number of forms are unable to produce their fructifications. *Coprinus stercorarius* and *C. plicatilis* show the phenomena of etiolation in the stipe, which grows to an exorbitant length when the fungus is grown in the dark

and no pileus is developed in the latter, while in *C. nycthemerus*, not even the first beginning of the development of the pileus can take place in the absence of light.

Reference has already been made to the influence of higher temperatures on the germination of certain fungus-spores, and there are several forms which require an increased temperature for developing their fructifications, principally those which are parasitic on warm-blooded animals.

The method of obtaining hanging-drop cultures containing single spores, a method which, as already mentioned, Brefeld was the first to adopt, is fully described. In employing this method with very minute spores which are difficult to find and observe, except under the higher powers of the microscope, the work may be facilitated by leaving the spores in a nutrient solution until the swelling which usually accompanies the first stages of germination takes place, when the spores are more easily seen. In dealing with spores which are wetted only with difficulty and hence show a tendency to cling together in groups on the surface of the liquid, keeping the spores for a time in a saturated atmosphere before transferring them to the liquid will usually overcome this disadvantage.

The growth of a fungus-mycelium in a hanging-drop culture may be prolonged after the food-material in the drop is exhausted, by absorbing the remaining liquid with a piece of sterilised filter-paper and adding a fresh drop of a nutrient solution.

Lastly, the various methods of artificial infection of the host-plant employed in working out the life-history of a parasitic fungus are described in detail.

The second and larger part of this volume deals principally with the special applications of the general methods of cultivation already considered to each of the different groups of Fungi. These applications are too varied to be noticed here and the reader must be referred for information to the volume itself. A general comparative account is also given of the morphology and biology of each group, and the evolution of and connection between the various forms of fructification, and the employment of these characters in classification are discussed.

One very useful feature in this part of the volume is that indications are frequently given where uncertainty or gaps exist in our present knowledge of the subject, and hence where research may be profitably directed.

Brefeld's well-known views on the phylogeny of the higher Fungi, which have frequently been put forward in his many publications, have, as is usually the case where questions of phylogeny are involved, led to much controversy and have been opposed by more than one conflicting opinion. They have been so often fully discussed elsewhere that it is unnecessary to enter into them here.

Suffice it to say that his idea of the origin of the ascus of the Ascomycetes from the sporangium of the Phycomycetes, in spite of its attractiveness, has not met with general acceptance, being opposed principally on cytological grounds. Furthermore, Brefeld refuses to recognise any sexual process as occurring in the Ascomycetes proper, with the exception of the nuclear fusion which

precedes the formation of the ascus. All the results of the investigations which have been carried out by various observers in recent years, and which show that, in addition to the karyogamy, a sexual process, either functional or reduced, still exists in several of the Ascomycetes, are regarded by him as erroneous and largely due to preconceived ideas.

It would unduly prolong the length of this notice to enter into a discussion on this matter, especially as the facts bearing on the question of the sexuality of the Ascomycetes have been reviewed on several occasions by those who have also themselves contributed important researches on the subject.

It is satisfactory to note that this veteran mycologist does not regard the present volume as the conclusion of his labours and we are promised at least two more volumes containing the results of further important researches, which will be awaited with much interest.

A.W.B.
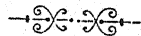
RECENT ADVANCES IN THE STUDY OF HEREDITY

(A Course of Lectures, for the University of London, delivered in the

Summer Term, 1909).

BY A. D. DARBISHIRE.

LECTURE V.

THE 1 : 2 : 1 AND 3 : 9 : 4 RATIOS.

FOR the theme of this lecture I propose to select the phenomenon of reversion, and to discuss the relation between this and dominance, and a possible alternative interpretation of the 1 : 2 : 1 proportion in F_2.

Hitherto we have been dealing with allelomorphic pairs of characters, the constituent unit-characters of which were independent of, and unaffected by, those belonging to other pairs of characters. In the case which I am about to describe, there is a specific and very definite effect exerted by a unit-character belonging to one allelomorphic pair upon a unit-character belonging to another allelomorphic pair.

Let us proceed to the description of the two parent types crossed. It will be remembered that in the description of the last cross we described a Pea, the markings on whose seed-coat consisted of a fine purple spotting on a grey background, and it will be remembered that in the F_2 generation, produced by crossing this with a maple Pea, there occurred a Pea in which this grey seed-coat existed without the purple spots. This grey seed-coat is a characteristic of many commercial varieties of *Pisum*, as for instance, many of the Field Peas. This grey is one of the characters used in the cross we are about to describe. The other character is that of the type of *Pisum* which has no pigment in its seed-coat at all. This has been the case in all the races which we have employed in crosses which concern cotyledon

characters, whether of shape or of colour; but we have had no occasion actually to refer to it. When a cross is made between a Pea with this grey coat and one with a white coat, the hybrid has a *grey coat with purple spots* and is exactly similar to one of the two forms involved in the last cross we described. When these Peas are allowed to self-fertilise there is produced a generation in which a proportion which is entirely new to us obtains. It is, actually, composed of *nine* plants with purple spot on grey background, *three* with grey coats only and *four* with white. There are two features of this cross which are new to us, *viz.*, the reversionary appearance of a character peculiar to the hybrid and possessed by neither of the parents, *viz.*, the purple spots; and the production of the three forms in this new proportion $9 : 3 : 4$ in F_2.

A theory has been put forward in explanation of these two results which is certainly consistent with what actually occurs. It is this. In this cross we are concerned with two allelomorphic pairs; one is grey and absence - of - grey, and the other is purple - spot and absence - of - purple - spot; but it is a characteristic of the purple spot that the mere presence of the factor for purple spot in the fertilised egg-cell which gives rise to a Pea plant is not sufficient to bring about the appearance of the purple-spots in the seed-coats of that plant. The factor for grey coat must also be present. Two factors therefore are necessary to bring about the appearance of this purple-spot character in the zygote. It further follows that the factor for purple spot, that is to say the dominant member of the pair, purple-spot and not-purple-spot, may exist in the zygote, without that zygote manifesting the purple spot; and the suggestion is that of the two forms involved in the cross we are describing, the grey Pea contains the factor for grey coat and the white Pea contains the factor for purple spot, but that this is not manifested because it is not associated with the grey coat. It will be seen from the application of this theory to this particular case that whilst the purple spot cannot exist without the grey coat the grey coat can exist without the purple spot; that is to say, whilst in this case two factors, only one of which can exist independently of the other, are necessary for the production of the purple spot, there are cases, as we shall see later, in which *neither* of the characters can exist independently of the other. But to return to the case before us. The grey-coated Pea contains the presence of grey coat and the absence of purple spot, whilst the white-coated one contains the *presence of purple spot* and

the absence of grey coat. The unexpected appearance of the purple spot in the hybrid will be seen to follow readily from the theory which we have enunciated. The two factors necessary for the production of purple spot, one of which existed in one of the parents and the other in the other, are brought together in the same zygote in F_1 and the manifestation of the purple spot is thus brought about. It will be seen how the phenomenon of reversion in this particular case is accounted for by this theory. Let us now proceed to see how it fits the results which obtain in F_2, and, later on, consider what justification there is for the conclusion that these phenomena are accounted for by this theory. For the factor for grey coat let us write G, and for the absence of this factor g; for the factor for purple spot let us write P and for the absence of this factor p. And let us assume that these pairs of characters segregate in gametogenesis in the same way as the other pairs of characters we have already dealt with. Inasmuch as this is a case in which two pairs of characters are concerned, we should expect a $9:3:3:1:$ proportion, in F_2, in which the characters are distributed as follows:—

$$9\ GP\ :\ 3\ Gp\ :\ 3\ gP\ :\ 1\ gp.$$

Let us now apply the theory, with which we started, to the F_2 result and see what will be the characters manifested by these four types of zygotes. The GP will be grey coat with purple spots, the Gp will be a grey coat without purple spots, but the gP will be a white Pea; in fact, it will be of the same zygotic constitution as the white Pea with which the cross was made, for according to the hypothesis the hybrid would not have manifested purple spots if the white parent had not been carrying the P factor. The gp is of course a white-seed-coated individual. The total result is therefore 9 individuals with grey coat and purple spot, 3 with grey coat only, and 4 with white seed-coats. Now although there is no external difference between the two kinds of white which make up this 4, *viz.*, the gP and gp, there is a great difference between the breeding capacities of the two kinds, inasmuch as the gP will, if crossed with grey coat, give rise to a purple spot on a grey coat in F_1; whilst the gp, when crossed with grey, should give simple dominance of grey.[1]

We have said that the theory which we are considering is

[1] Of course there are two types of gP, viz. $ggPp$ and $ggPP$ (there being two of the former and one of the latter in every three). The former when crossed with grey, will give grey and grey with-purple-spot in equal numbers. The latter will give all greys with purple spots.

consistent with the results both in F_1 and F_2; but we did not commit ourselves to the conclusion that this was a demonstration of the correctness of this theory. It will, however, be seen that the theory readily admits of being tested; what I mean is this:—the existence of 4 whites in every 16 in F_2 is consistent with the theory put forward to account for this case, but we should not rest satisfied with it until we have obtained more evidence that these two types of whites really do exist within the four. All that has to be done is to cross the whites which appear in this generation with pure greys. Those carrying P, that is to say 3 in every 4, should give purple spots in F_1, whilst those of the formula gp should give simple dominance of grey.[1]

This experiment is not a difficult one to carry out, because there is a correspondence between the colour of the flower of the plant and the characters of the seed-coat which will be manifested when the fruit is ripe. Plants which will produce GP and Gp seed-coats always have purple flowers, whilst plants which will produce white seed-coats, whether of constitution gP or gp always have white flowers; so that it is possible to know whether the plant will have white seed-coats or not, by the colour of its flowers; although this does not enable one to determine whether, if coloured, they will be GP of Gp.

I have myself made, this year (1909) a number of crosses between these extracted F_2 whites and certain pure and extracted grey types. The only fact which affords some kind of clue as to what the result will be, suggests that it will be in a direction contrary to that expected by the theory we have considered. I refer to the fact that hitherto, so far as I have been able to discover, all crosses between greys and whites have given F_1 with purple spots, which means that all of the whites used must have been of the formula gP. That is to say, supposing the whites employed in such crosses may be considered as fairly representative of white-coated Peas in general, none of the white-coated varieties on the market are pure white, *i.e.*, of formula gp; and the difficulty of imagining any *à priori* reason why they should not be so, suggests that the Mendelian hypothesis put forward to explain this case may not closely represent what actually occurs. This, however, is only a very faint indication, and will, of course, count for nothing as against the result of the experiment which I said I am conducting. I have dealt somewhat fully with this case for a number of reasons. In the first place it is an instance of the

explanation of a reversionary phenomenon by Mendelian theory; in the second place it is one that can easily be repeated by anyone anxious to witness the facts for himself. There is, of course, no difficulty in obtaining a white-seeded Pea, and a field Pea with grey seed-coats can be obtained from or procured by any corn-chandler. This case also has a peculiar interest from the more general point of view of the interpretation of natural phenomena, in that it is a case in which we are not held up at one particular point where all we can say is that the theory put forward is consistent with the facts, and that we have no further demonstration than this that the theory approximates to the true explanation of them. In this particular instance all we can say when we have raised F_2 is that the theory put forward is consistent with the results obtained; but we can proceed to discover whether or no this is a proof of the correctness of the theory by further experimentation with the four whites, as explained above.

Again, the ratio 9 : 3 : 4 itself is interesting in more than one way. It will be seen that if we classify the GP and the Gp together as Peas with pigmented seed-coats, and refer to the white ones as unpigmented, there are twelve coloured to four colourless, *i.e.*, *three* coloured to *one* colourless. The procedure of lumping together the GP with the Gp is not a mere artificial association of two categories having nothing to do with one another for the purpose of obtaining a particular numerical ratio, but is justified by the fact that the Peas which we have described as grey do, as a matter of fact, bear very faint purple spots; so that the difference between GP and Gp is not the difference between a grey Pea which bears a purple spot and one which bears none, but between a Pea which bears a pronounced purple spot and one which bears a faint one. This fact is a curious one, when we consider it in relation to the theory of the gametic constitutions of the two types involved in the cross which has produced this result; for the faint (as it were, suppressed) purple spot, is borne by that of the two parents, namely the grey Pea, which carries the *recessive* member of the pair, purple spot and its absence, whilst the parent, namely the white Pea, which bears the *dominant* member of this pair, the factor for purple spot itself, exhibits no trace of this character whatsoever. And this fact would again suggest that the explanation of the phenomena which this cross presents may not be so simple as the Mendelian one which we have considered.

There is another respect in which this ratio 9 : 3 : 4 ; is an

interesting one. Bateson has suggested that many cases, which in the early days after the rediscovery of Mendel's papers, were interpreted as instances of a 1 : 2 : 1 proportion, may in reality have been instances of a 3 : 9 : 4 proportion; for it is obvious that if the numbers from which the ratio is calculated are not very great, it will not be easy to determine whether a particular ratio is to be classed as 1 : 2 : 1 (or, as we may call it, 4 : 8 : 4 for the moment), or as 3 : 9 : 4; especially when it is remembered that many Mendelian investigators are, quite rightly in many cases, contented with a qualitative as opposed to a quantitative result. But now that it is known that this 9 : 3 : 4 or 3 : 9 : 4 proportion is sometimes attained, it becomes extremely important to determine whether the ratio in any given case is of the 1 : 2 : 1 or 3 : 9 : 4 type, because, of course, the causes underlying these two proportions are entirely different. And it becomes important, therefore, to breed one's material on so large a scale that there can be no question to which of these two types the ratio obtained belongs. The determination of this point is not a question of individual arbitrary taste, but is based on a statistical formula which we shall come to consider later on.

The suggestion that some ratios which were interpreted in the first place as instances of the 1 : 2 : 1 type might really be instances of 3 : 9 : 4, raises the question in one's mind whether *all* cases of 1 : 2 : 1 may not be of the 3 : 9 : 4 type. This suggestion of course strikes at the root of Mendelian principles, and if an examination of the ratios obtained, by the statistical formula to be described, prove that the proportion 1 : 2 : 1 never occurs, the most elementary and fundamental tenets of Mendelian doctrine will have to be given up. For instance it is obvious that no case of Mendelian inheritance can be explained on a hypothesis involving a single pair of characters; and that all instances of the common Mendelian phenomena of dominance and segregation, in the 3 : 1 proportion, are to be explained by a hypothesis relating to two pairs of factors, one of which (as in the case of the seed-coats in *Pisum*) demands the co-existence in the zygote of two factors for its manifestation. If some theory of this kind should, after experimental and statistical analysis, prove to fit the facts more closely than the one at present held, we should, I think, at least have a theory which helps to explain the phenomenon of dominance; for it has long seemed to me, long in fact before the 9 : 3 : 4 proportion was known, that dominance is merely a type of reversion. My idea has been somewhat as follows :—When two

remotely related forms are crossed the equilibrium of both is disturbed to so great an extent that the hybrid has, so to speak, to go a long way back before it can get a firm foothold again,[1] and then we get a case of what we call reversion. But if the two forms are not so remotely related the disturbance is not so great and the result is that the hybrid does not fall further back than on one of the two parents, and we get what we call dominance. The difference between the two cases may be expressed in another way, which will be more repulsive than the last to those who think that sober ratiocination is the only method of elucidating the truth. In the case of a cross between remotely connected forms, the disturbance caused by their union is so great that neither of them can keep their heads, with the result that the hybrid reverts to the first solid thing in the memory, that is to say the racial memory, of the zygote; whereas in the case of the union of two closely related forms the disturbance is not so great that one of them at least cannot keep its head and impress its characteristics upon its off-spring. I am quite aware of course that an idea of this kind will be rejected as unscientific; but the idea rose up in my mind as I was paying attention to the point in question and I am not by any means convinced that an apparently extravagant analogy of this kind is any more remote from the real state of affairs than the hypotheses which find favour with modern professional men of science. It is, however, perhaps advisable to return to the conventional sphere of thought. An objection which is likely to be raised straight away to the suggestion that there is no such thing as a 3 : 1 or a 1 : 2 : 1 proportion, and that all of them are really instances of 3 : 9 : 4 is, that in all cases of 3 : 9 : 4 the hybrid is a reversionary one, *i.e.*, it bears the character of some remote ancestor, so that the result of F_1 is amply sufficient to prove not only that it belongs to one or the other category, and hence that the two are radically distinct, but also to which of the two it belongs. The answer to this is, in the first place, that the ratio 1 : 2 : 1 is not always associated with simple dominance in F_1, as in the case of the Andalusian fowl. Inasmuch therefore as the character of the Andalusian may be dependent for its manifestation on the co-existence in the zygote of two factors, one of which existed in the splashed white and the other in the black, there is nothing but an estimation of the ratio by the statistical formula referred to to show

[1] The answer to the complaint, which the reader may make, that this is too metaphorical is that the signification of the terms heredity and reversion are as metaphorical as can be.

that this case is not precisely parallel to that which we have described in the inheritance of the characters of the seed-coat in *Pisum*.

The other answer to the imaginary objection to the suggestion that all cases which are now explained on the hypothesis of a single pair of characters are really cases of 3 : 9 : 4, the objection that in all cases of 3 : 9 : 4 the hybrid is reversionary is contained in the following question. Do we know that such a thing as simple dominance *ever* occurs? Can we be certain that the apparent similarity of hybrid and dominant parent is not due to our inability to detect the differences between them? In the case of roundness and wrinkledness in Peas, the first character on the list of the seven with which Mendel dealt, the answer to this question is—no. For we now know that although the hybrid round and its round parent are indistinguishable to the naked eye, they differ radically from one another in two characters. A figure was given in my last lecture of the starch grains which distinguish these two types of Peas, and I give here a figure of the starch grains of the hybrid round. A reference to the figures of the parental types of grain will show that those of the round are single and nearly twice as long as broad, whilst the grains of the wrinkled Pea are compound and almost round, the number of component pieces varying between 2 and 8, the commonest number being 6. The grain of the hybrid Pea is, as will be seen from the figure given here, almost exactly intermediate between its two parental types. Its length-breadth index is intermediate; and the compoundness of the grains in the aggregate is intermediate. In the first place (in the case of the Pea from which the grains figured were taken) about half the grains are compound and half single; and the compoundness in those that are compound is intermediate between singleness on the one hand and the degree of compoundness exhibited by the grains of wrinkled Peas on the other. For whilst in these latter the number of component pieces ranges between 2 and 8 and the commonest is 6; in those of the hybrid Pea the number ranges from 2 to 4 and the commonest is 3. Again, mention was made in my last lecture of the difference in the absorptive capacity in the two types of Pea; the absorptive capacity of the hybrid round Pea is very nearly intermediate between that of its two parents. It will be remembered that the absorptive capacity of a set of round Peas was given as 86%, and that of a set of wrinkled ones as 120%. The absorptive capacity of a Pea derived from the

union of these two types is 100%, which is a fairly close approxi-mation to intermediateness. I do not mention these two points of difference as being two distinct characters in which the hybrid round is intermediate between its two parents; on the contrary I
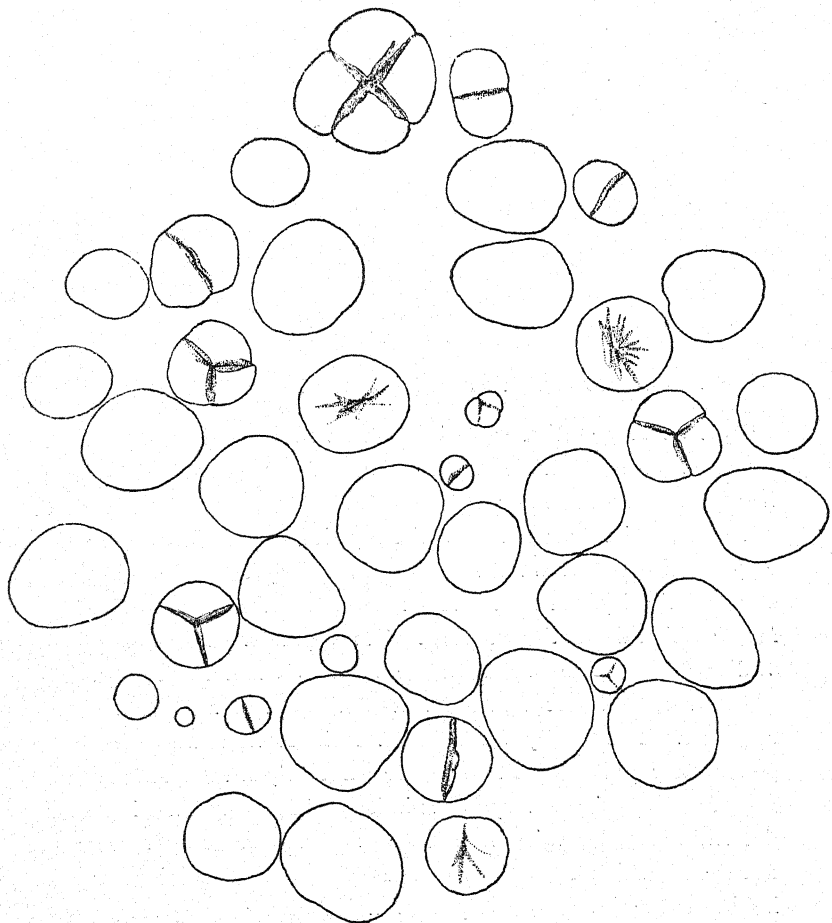
Fig. 3. Starch Grains of a Hybrid Round Pea.

[I wish to express my thanks to the Council of the Royal Society for permission to reproduce this figure.]

imagine that the absorptive capacity and the structure of the grains are very intimately connected.

We see therefore that in the case of the very first character dealt with in Mendelian investigation, that which we took, from an examination of externals, to be an instance of simple dominance,

proves on closer investigation to be a case in which the hybrid is intermediate between the two parents. And the question whether all cases of dominance may not be due to the fact that we have not yet succeeded in detecting the differences between the hybrid and the parent from which it is apparently indistinguishable, presents itself most forcibly to the mind.

LECTURE VI.

The Mendelian Inheritance of Sexual Characters.

RECENT genetic research has thrown a flood of light on the nature and mode of inheritance of sex. In the first place it has practically demonstrated the correctness of the view that the sex of an animal or plant is already determined in the fertilized egg-cell; in the second place, the probability that there is a very close similarity between the Mendelian unit-character and the factor which determines the sex of an organism puts us in the way of discovering the essential nature of one of these two things.

Let us deal first with the first of these two results of genetic research. The theory of sex which until recent years had met with general acceptance was that the sex, not only of the fertilized ovum, but of the growing embryo, was indeterminate and that it was not determined until a fairly late stage in development by factors, the nature of which then became the subject of discussion. It was held that the developing organism maintained the balance between the two sexes, that its sex was, as it were, up to a certain moment in development, poised on a knife-edge, and that at this point external stimuli of some kind resulted in its falling off on one side or the other, *i.e.*, in its becoming a definitive male or female. One result of the prevalence of this theory was that all work on the determination of sex consisted in testing hypotheses as to the nature of the stimuli which resulted in the production of males and of those which resulted in the production of females. Schenk's experiments with man and Yung's with tadpoles are among classical instances

of attempts to deal with the problem on these lines. The work based on this conception achieved apparently conclusive and immediate results, because certain elementary conditions necessary to experiments of this kind were disregarded ; and it gave distinct colour to the generalization, advocated in Geddes and Thomson's "Evolution of Sex," that the production of males is determined by general katabolic conditions and that of females by anabolic ones. Yung, for instance, found that favourable conditions of nutrition resulted in the production of a high percentage of males in a batch of tadpoles ; and that opposite conditions resulted in a correspondingly high proportion of females. In experiments of this kind it is essential that a record of the number of individuals at the beginning and at the end of the experiment is kept, because, if this is not done, there is no means of knowing whether the high final percentage of one sex is due to a particular effect produced on the sexless embryo *in all cases*, or whether it may not be due to a differential death-rate resulting from the abnormal experimental conditions. No experiment of this kind is of the slightest value unless a record of the total number of individuals at the beginning and at the end of the experiment is kept.

The cause of the existence of this theory of the determination of sex is to be sought in a too cautious inference from the facts of development. The sex of an animal or plant is not discernible in the fertilized egg-cell which gives rise to it ; nor are the structural features which distinguish the sexes manifested until fairly late in development. And any inference, from these facts, that the sex of the adult was already determined in the fertilized egg-cell which produced it, ran an obvious risk of being objected to as being too far in advance, or ahead, of the facts. This objection is in our opinion a legitimate one ; and the way out of the difficulty is that the facts of the development of primary and secondary sexual characters do not constitute the basis from which we should start in elaborating a theory of the determination of sex. I say this is a way out of the difficulty. But I am by no means convinced that these facts ought to be neglected in the consideration of this question.

The theory that the sex of an organism is already determined in the fertilized egg-cell from which it develops has become widely adopted of recent years because the suggestion that sex is inherited in Mendelian fashion has received very general credence.

This suggestion was bound to be made sooner or later. The

parallel between the mode of inheritance of the two sets of characters, and between the characters themselves is very close. Mendelian and sexual characters are both inherited in an alternative manner, that is to say the offspring resemble one of their two parents to the exclusion of the other. The details of the similarity between the mode of inheritance of Mendelian and that of sexual characters do not concern us now. The point is that the two things are similar; and that a theory of the mode of inheritance of Mendelian characters was in the field before a theory relating to sexual characters. So that the obvious fact of the close similarity between the two phenomena has given birth to the theory that sexual characters are Mendelian in their mode of inheritance. If a theory of the inheritance of sexual characters had been in the field first, this same fact would have resulted in the enunciation of a theory that the inheritance of Mendelian characters is similar to that of sexual characters. Of course the discovery of the mode of inheritance of sexual characters is a more interesting result than is that of Mendelian ones. So that the latter discovery would have received far less attention than the discovery of the mode of inheritance (assuming for the sake of the argument that it has been discovered) of sexual characters has done. I lay emphasis on this point in order to show that the explanation of a phenomenon (such as sex in this instance) is nothing more than a description of it in terms of a theory which happened to be in the field before it.

The first organized attempt to demonstrate the Mendelian inheritance of sexual characters is that of Castle,[1] enunciated in 1903 in the following words, " Sex in diœcious animals and plants is inherited in accordance with Mendel's Law; that is, in accordance with principles of dominance and segregation. The ordinary diœcious individual is a sex-hybrid or ' heterozygote ' (Bateson), in which the characters of both sexes are present, one dominant, the other recessive. In the male, the female character is recessive, and conversely in the female, the male character; but each sex transmits the characters of both.

The existence of each sex (in a latent condition) in the other is shown by the occurrence in each sex of rudimentary organs peculiar to the other."

Professor Castle then proceeds to give some cases which demonstrate the latency of the characters of one sex in the opposite one, and meets the possible objection that many of them may be

[1] Bull. Mus. Camp. Zoology, Harvard, Vol. XL., No. 9.

cases of imperfect or potential hermaphroditism by a free admission that this may be so. Indeed he would even go further, he says, and say that all animals and plants " are *potential* hermaphrodites for *they contain the characters of both sexes.*"

We must proceed with great caution here; and before we continue with Professor Castle's theory let us make ourselves as clear as we can about the signification of the terms employed.

A Mendelian hybrid and a hermaphrodite, as the terms are commonly understood, are very different things, if we do not confine our attention to superficial points of similarity.

The essential nature of a Mendelian hybrid, as commonly understood, may perhaps be best expressed in the statement that the only difference between it and a dominant, in those cases where the two are externally indistinguishable, is that all the gametes of the dominant bear the D factor, whilst only half of the gametes of the hybrid bear the D factor, the remainder bearing the R factor. This at any rate is what may be called the extreme Mendelian or rather Weismann-Mendelian view; whether it is actually held by any Mendelian workers is a question beside the point. This view represents the logical conclusion of the Weismannian doctrine that the characters of an organism are determined solely by the potentialities existing in the germ-cells which gave rise to it. The soma is a mere vehicle for the germ-plasm which it protects. It is not affected by the characters borne by the germ-cells which it contains, any more than these characters are determined by the soma in which the germ-cells which bear them are lodged.

All therefore that we mean, if we hold this view of the Mendelian hybrid, when we say that the characters of the recessive are latent in the heterozygote is that half of the germ-cells of the heterozygote bear the recessive character.

Now a hermaphrodite is a very different thing from a Mendelian hybrid in the sense just explained. An actual, as opposed to a potential, hermaphrodite is of course an entirely different thing, inasmuch as the characters of both sexes are manifested side by side in its soma. But there is almost as profound a difference between a potential hermaphrodite and the kind of Mendelian hybrid of which we have been speaking. In the hermaphrodite the characters of the two sexes are blended in the somatic organization of the individual; those of one sex however remain latent.

The Mendelian view of the nature of the hybrid outlined above is probably held most largely by those whose familiarity with these

ideas is only derived from text-books. But there is another view, which probably more closely resembles that held by experts, and which comes much closer to the conception of a sexual hermaphrodite. I have already said, in an earlier lecture, that the formula DR may relate either to the nature and proportion of the kinds of germ-cells borne by a zygote; or to the somatic organization of the zygote itself. The former alternative corresponds to the Mendelian view which we discussed first; the latter to the view which as I have said approaches more closely the conception of a sexual hermaphrodite.

This second view is involved in the idea that every zygote is a double structure, as opposed to the gamete which is a single one.

According to this view, the statement that the recessive character is latent in the heterozygote means not only that half of its germ-cells bear the recessive characters; but that the recessive character actually exists potentially in the somatic organization of the heterozygote itself. It is important to bear these two Mendelian views of the nature of the hybrid (and indeed of the zygote in general) distinctly in mind, because our interpretation of certain phenomena of sex (*e.g.*, the appearance of rudimentary structures characteristic of the opposite sex) will be determined by the form of Mendelian theory we start with.

To return to Castle's theory. He assumed that every individual in a diœcious species was a sex hybrid and produced ♂ and ♀ germ-cells in equal numbers. The result of the union of any large number of ova and spermatozoa at random would therefore be as follows:—

$$\text{♂} + \text{♀ (ova).}$$
$$\text{♂} + \text{♀ (spermatozoa).}$$
$$1 \text{ ♂ ♂} : 2 \text{ ♂ ♀} : 1 \text{ ♀ ♀ (zygotes).}$$

Now Castle supposes that pure sex zygotes of the type ♂ ♂ and ♀ ♀ do not exist, and supports this supposition by analogical reasoning. The only fertile unions of gametes are, therefore, those between ova and spermatozoa bearing dissimilar sexes. All zygotes are therefore heterozygotes as regards sex: they are the result of the union of dissimilar gametes; and the gametes which they produce are of the same two kinds. The principle of alternative dominance has to be invoked to explain the fact that these sex-heterozygotes may be either "males" or "females." And herein lies the chief weakness of the theory; the production of the two sexes in approximately equal numbers receives a most unsatisfactory explanation.

The theory which has superseded Castle's and seems in much

closer harmony with the mode of inheritance of sexual characters, is that the members of one sex are heterozygous as regards their sex; whilst those of the other are pure recessives. This theory provides a very simple explanation of the production of the two sexes in equal numbers; the result of the mating DR × RR being, of course, DR and RR in equal numbers. The facts which have been brought to light by the study of the inheritance of Mendelian and of sexual characters and by the study of the cytological phenomena in certain insects all strongly support this view; but the evidence derived from these several sources is strangely conflicting. Our conclusion therefore is that one sex is a heterozygote and the other is a pure recessive; but the evidence on the question which is the heterozygote and which is the recessive is not at present conclusive.

The conclusion reached by the experimental treatment of this problem by means of breeding experiments is that the female is the heterozygote and the male the recessive. Let us consider two classical cases which support this view; and let us deal first with Correns' crosses of *Bryonia*. Correns made a number of crosses between *Bryonia dioica* and *Bryonia alba*, which is monœcious.

B. dioica ♀ × *B. alba* gave " F$_1$ females, with or (usually) without occasional male flowers. The observed numbers from this mating were 989 females, with 2 males which must be regarded as exceptional."

B. alba (monœcious) used as a female × *dioica* ♂ gave an F$_1$ consisting of males and females in approximately equal numbers. Correns offered an explanation of these phenomena which involved the assumption that maleness was dominant, that is to say that the *male* is heterozygous and the female pure recessive. The zygotic constitution of the male is ♂ ♀, and of the female ♀ ♀. The male and female cells of *alba* are supposed to be undifferentiated in respect of sex. Correns' theory may be summarised as follows:—

> *dioica* ♀ is ♀ ♀.
> *dioica* ♂ is ♂ ♀.
> *alba* ♀ is ☿.
> *alba* ♂ is also ☿.

Thus when normal *dioica* mate *inter se* the mating and its result may be represented as follows:—

> *dioica* ♀ × *dioica* ♂ gives rise to females ♀ ♀ and males ♀ ♂

The first cross we considered would be *dioica* ♀ × *alba* ♂ giving rise to all females of the form ♀ ☿.

The second cross :—

alba ♀ × *dioica* ♂ giving rise to females ♀ ☿ and males ♂ ☿.

Bateson has suggested a simpler theory which does not involve the assumption of a special factor for the monœcious character, and in which the *female* is heterozygous.   It is as follows :—

> *dioica* ♀ has egg-cells ♀ and ♂.
>
> *dioica* ♂ has pollen all ♂.

alba ☿ has egg-cells ♀ and ♂; and pollen all ♀.

The above matings would then give the following results :—

dioica ♀ × *dioica* ♂ gives females ♀ ♂ and males ♂ ♂.

dioica ♀ × *alba* ♂ gives pure females ♀ ♀ and heterozygous females ♀ ♂.

alba ♀ × *dioica* ♂ gives females ♀ ♂ and males ♂ ♂.

The reader is referred to Professor Bateson's *Mendel's Principles of Heredity*, p. 168, for a detailed justification of the assumptions involved in his hypothesis.

Let us now proceed to a consideration of the remarkable case of *Abraxas grossulariata*—the common yellow, black and white moth that infests our currant and gooseberry bushes—which has been worked out by Raynor and Doncaster.   There is a variety of this moth the character of which is fairly well conveyed by the name which has been given to it—var. *lacticolor* : it differs from the normal type in the great reduction in the size of the black spots. The type and its varieties are figured on Plate I. (facing p. 44) of Professor Bateson's *Mendel's Principles*.   This *lacticolor* variety is known exclusively as a female.

The following crosses between it and the normal species were made, and gave the results indicated :—

1.   *lact.* ♀ × *gross.* ♂ gave F_1 ♂ s and ♀ s, all *gross.*

2. F_1 *gross.* ♀ × F_1 *gross.* ♂ gave *gross.* ♂ s and ♀ s, and ♀ *lact.*; no male *lact.* being formed.

3.   *lact.* ♀ × F_1 *gross.* ♂ gave all four possible types, viz., *gross.* ♂ s and ♀ s; and *lact.* ♂ s and ♀ s; the *lacticolor* males being the first ever seen.

4. F_1 *gross.* ♀ × *lact.* ♂ gave all ♂ s *gross.* and all ♀ s *lacticolor.*

The theory by means of which Doncaster sought to account for these remarkable phenomena was based on Castle's theory of sex, according to which *each* sex is a heterozygote in respect of sex. It embraced the following hypotheses :—

1.   Each sex gives off ♂ - and ♀ -bearing gametes.

2.   In ♀ s which are heterozygous in respect of colour, gametic

coupling occurs in such a way that the *gross.* character is associated with maleness, and the *lacticolor* character with femaleness.

3. In the ♂s which are colour heterozygotes no such coupling occurs.

4. There is a preferential mating amongst the gametes, such that a union can only take place between ♂- and ♀-bearing gametes.

5. Dominance is determined by the female parent.

Bateson has put forward a much simpler explanation of these phenomena, which, like his theory in explanation of Correns' results with *Bryonia*, starts from the assumption that femaleness is dominant. His theory is as follows :—

1. The female is heterozygous in regard to sex, femaleness being dominant; the male is a homozygous recessive.

2. In the gonads of the hybrid in which the two dominant factors femaleness and the *gross.* character co-exist there is spurious allelomorphism between these two dominant factors, that is to say each gamete may bear one of these factors, *but not both.* The following analyses of the matings shows that the actual results follow from this theory :—

1.

$$lact. ♀ \quad × \quad gross. ♂$$
$$RR ♀♂ \quad | \quad DD ♂♂$$

F$_1$ *gross.* ♂   *gross.* ♀
   DR ♂♂   DR ♀♂

2.

        F$_1$ *gross.* ♀   ×   F$_1$ *gross* ♂.
composition   DR ♀♂   DR ♂♂
gametes { D♂   {D♂
            R♀   {R♂

2 *gross.* ♂   1 *gross.* ♀   1 *lact.* ♀
DR ♂♂   DR ♀♂   RR ♀♂
DD ♂♂

3.

         lact. ♀   ×   F$_1$ *gross.* ♂
         RR ♀♂ | DR ♂♂

1 *gross.* ♂   1 *gross.* ♀   1 *lact.* ♂   1 *lact.* ♀
DR ♂♂   DR ♀♂   RR ♂♂   RR ♀♂

4.

         F$_1$ *gross.* ♀   ×   *lact.* ♂

gross. ♂   *lact.* ♀
   DR ♂♂   RR ♀♂
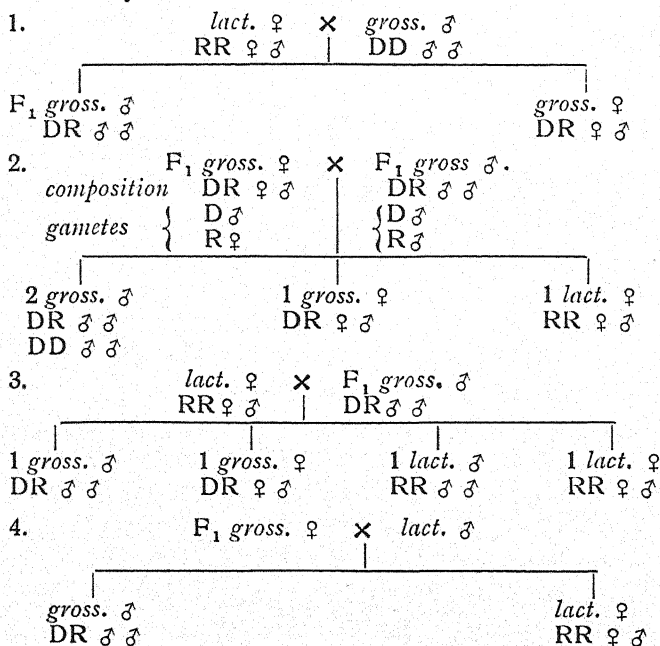
The following Tables exhibit the above mating in a form which I find is more easily intelligible :—

1.

gross. ♂
gametes

	D ♂	D ♂
R ♀	*gross.* ♀ DR ♂ ♀	*gross.* ♀ DR ♂ ♀
R ♂	*gross.* ♂ DR ♂ ♂	*gross.* ♂ DR ♂ ♂

lact. ♀   *gametes*

The lower formula in each square indicates the zygotic constitutions of the resultant zygotes. *D* stands for the *gross.* character; *R* for the *lacticolor*; ♂ for maleness (recessive), ♀ for femaleness (dominant). The upper formula in each square gives the somatic appearance of the zygote.

2.   F₁ *gross.* ♂

	D ♂	R ♂
D ♂	*gross.* ♂ DD ♂ ♂	*gross* ♂. DR ♂ ♂
R ♀	*gross.* ♀ DR ♀ ♂	*lact.* ♀ RR ♂ ♀

F₁ *gross.* ♀

3.   F₁ *gross.* ♂

	D ♂	R ♂
R ♂	*gross.* ♂ DR ♂ ♂	*lact.* ♂ RR ♂ ♂
R ♀	*gross.* ♀ DR ♀ ♂	*lact.* ♀ RR ♀ ♂

[*lact.* ♀

4.

The top table:

F₁ *gross.* ♀	*lact.* ♂	
	R ♂	R ♂
D ♂	*gross.* ♂ DR ♂ ♂	*gross.* ♂ DR ♂ ♂
R ♀	*lact.* ♀ RR ♀ ♂	*lact.* ♀ RR ♀ ♂

Doncaster has recently made a discovery of extraordinary interest.

The above experiments are incomplete inasmuch as the mating:— *WILD gross.* ♀ × *lact.* ♂ had not been made; only F₁ *gross.* ♀ × *lact.* ♂ (see No. 4). The result of this cross is now known; and the result of the cross between the *WILD gross.* and *lact.* ♂ is precisely the same as the result of the cross between F₁ *gross.* ♀ × *lact.* ♂, namely, in both cases, *gross.* ♂s and *lact.* ♀s. In other words the ordinary wild *grossulariata* in districts where *lacticolor* is unknown are in reality a race of which the males are pure *gross.*, though the *females are in reality hybrids of lacticolor*, and so continue from generation to generation.

Normal ♀ *gross.* and the F₁ ♀ *gross.* from *lact.* ♀ × ♂ *gross.* are identical in composition. Whether a *gross.* ♀ has *gross.* ♀ or a *lact.* ♀ for a mother makes no difference to its properties.

gross. ♂	*gross.* ♂	
	D ♂	D ♂
D ♂	*gross.* ♂ DD ♂ ♂	*gross.* ♂ DD ♂ ♂
R ♂	*gross.* ♀ DR ♀ ♂	*gross.* ♂ DR ♀ ♂

Well may Bateson remark "This fact is one of the most striking to which genetic research has yet led."

In the case of both *Bryonia* and *Abraxas* the theory which gives the simplest explanation of the facts is that the female is a heterozygote (femaleness being dominant) and the male a homozygous recessive. This conclusion is supported by the facts of sex-limited heredity. The nature of this phenomenon can most easily be made clear by describing a concrete instance in which it is manifested.

In the Dorset Horned sheep the horns are well developed in both sexes. In the Suffolks horns are not developed either in the rams or the ewes. When individuals of these two races were crossed, it was found that the F_1 male lambs had horns of fair size whilst the F_1 ewes were hornless. The horned character may therefore be said to be dominant in males but recessive in females. We are probably nearer the truth if we say that there is something in the female which suppresses the character—which limits the apparent inheritance of that character to the male sex—and that the male lacks this something.

The same phenomena are exhibited by the inheritance of colour-blindness. About 4% of the males in European countries are colour-blind; whereas less than ·5% females are. Colour-blindness is transmitted chiefly to sons, very rarely to daughters; but the non-colour-blind daughters frequently transmit it to their sons again. There appears, therefore, to be some factor in the organization of the female which suppresses the colour-blind character, just as it suppressed the horned character in the sheep.

It follows that women can transmit colour-blindness without having it; whilst men cannot.

It is argued that this proof that the females possess this "suppressing" factor which is absent from the male, supports the theory that femaleness consists in the presence of something whilst maleness is determined by the absence of that something. Female-*ness*, therefore, is dominant; whilst male*ness* is recessive. But "a female" is a heterozygote, half of her gametes bearing maleness, and half femaleness; whilst a "male" is a homozygous recessive.

The evidence which we have considered so far is consistent with the theory that the *female* is the heterozygote. In the next lecture we shall deal with facts which, whilst they support the theory that one sex is heterozygous and the other homozygous, point to the *male* as the heterozygote and the female as the homozygote.

OBSERVATIONS ON PHYCOERYTHRIN, THE RED PIGMENT OF DEEP-WATER ALGÆ.[1]

By E. K. Hanson.

[Plate V.]

THE red colouring matter of deep-water algæ possesses considerable interest, especially in regard to two points :—

1. Its rôle in assimilation.
2. Its chemical nature, suggested to be protein.

These problems have not been satisfactorily settled, and the following investigation was therefore undertaken to obtain some light, if possible, on these matters.

Very great difficulty has been encountered, however, in the preparation of material. The colouring matter occurs in very small proportion in most of the red algæ, and those which yield any reasonable quantity are only to be obtained under favourable tidal conditions in very few localities in the British Isles. Various species of *Ceramium*, especially *Ceramium rubrum*, alone of the weeds used, gave a fair quantity.

In addition, the pigment is soluble only in water, and the aqueous extract contains gummy substances from which it is necessary to purify the colouring matter, as far as possible, for chemical investigation. As the phycoerythrin on precipitation passes very easily into an irreversible " gel," the method of repeated re-solution and re-precipitation for purification is not practicable. The precipitate is also extremely difficult to filter, filtration being extremely slow even under pressure, so that prolonged exposure to the precipitant is unavoidable, and this exposure appears to accelerate the formation of the irreversible gel. Attempts were made to avoid this effect by keeping the filtering solutions at 0°C by means of an ice-jacket, but though this cooling delayed the formation of insoluble gel, it did not prevent it.

The solid material used for the experiments below was therefore obtained by fractional precipitation with alcohol, but it can only be regarded as a very rough approximation to the pure colouring matter : as will be seen it contains a high percentage of ash.

The weed was gathered and despatched to me with the least possible delay, and on arrival was immediately washed free from

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[1] A short account of these observations was given to the Chemical Society, and an abstract has been published. Proc. Chem. Soc., 1909. 25. 117.

sand and salt water, with tap water. Only very slight loss of pigment occurred in this process. The wrung out weed was then placed in large bottles (about 5 litres capacity) and the bottles were filled with distilled water with a few drops of chloroform, securely corked, and placed in a warm spot. In a few hours' time the red colour began to pass out of the cells into the water, and in a couple of days' time, practically all the phycoerythrin had been extracted. The solution so obtained was filtered through glass wool, and the filtrate was used for the optical experiments and for those with digestive ferments. It possessed a rose colour with a strong orange fluorescence. It putrifies rather quickly unless some powerful antiseptic is present, but, if kept sterile, it is more resistant both to light and air than previous investigators have recorded. Various antiseptics were tried, including phenol, thymol, chloroform, carbon tetrachloride, and eucalyptus oil; the last mentioned proved by far the most effective: metallic salts, *e.g.*, mercuric chloride, are not available, as they produce an effect on the colouring matter.

For the solid material, the simple extract was concentrated to about one-third its original bulk by distilling under a pressure of a few cms., the temperature not rising over 38°C. Usually in this process a little brown-red precipitate was formed, but the solution retained its rose colour and orange fluorescence. Any precipitate was filtered off, and methylated spirit was then added until the fluorescence disappeared, the solution was allowed to stand, and the precipitate was filtered off. More alcohol was added to the filtrate until most of the red colour had gone, and this fraction (much the largest) was allowed to settle, the supernatant liquid poured off, and the residue washed several times by decantation with 70% spirit, and then transferred in the pasty state to a large clock glass and dried in a vacuum dessicator over sulphuric acid. This process was adopted partly on account of the extreme tediousness of ordinary filtration, and partly because the precipitate, being of a gluey nature, was found to stick to the filter paper, involving either a heavy loss or contamination with filter paper fibre.

An attempt was made to obtain purer phycoerythrin by drying the washed weed in a calcium chloride oven at the ordinary temperature; the dried weed was then powdered and extracted with various solvents. But it was again found that only water took up any phycoerythrin, and even water dissolved the phycoerythrin from the dried weed very slowly, and only very dilute solutions could be obtained: the method was, therefore, abandoned.

The Part Played by Phycoerythrin in Assimilation.

As the algæ in which phycoerythrin occurs contain also chloro-
phyll, and yet live at a depth where the light reaching them is largely
deprived of that portion of the spectrum most efficient in forwarding
assimilation in chlorophyll-bearing plants, it has been suggested
that the role of phycoerythrin is to aid assimilation by handing on
the energy derived from the absorption of the light reaching the
depths at which these algæ grow. If this is so, the absorption
spectrum of phycoerythrin should exhibit marked absorption of the
blue-green light which is available in deep water, and, further, it
must in some way transmit the energy thus obtained to the chloro-
phyll. From the deep orange fluorescence it is conjectured that
phycoerythrin absorbs the blue-green light and degrades it to yellow
and red which can be absorbed in turn by the chlorophyll.

The absorption spectrum of phycoerythrin has been exhaustively
studied by F. Schütt,[1] and it has been shown that phycoerythrin
does indeed absorb that part of the spectrum which penetrates deep
water. A photograph of the phycoerythrin absorption spectrum is
shown in Plate V., Fig. 2.

Schütt[2] has also shown that only light of wave-length 600-486
has the power of exciting fluorescence in phycoerythrin solutions,
and advances the opinion that the fluorescent light is probably
about 590-560, *i.e.*, near the sodium (D) line. But no exact deter-
mination appears to have been made, up to the present, on the
fluorescence, and so the fluorescent light from phycoerythrin solution
was photographed.

The method employed was to send a beam of light through a
trough containing phycoerythrin solution and to place the spectro-
scopic camera at right angles to the path of the beam. "Pan-
chromatic" plates were used which were almost equally sensitive
to all parts of the spectrum, though slightly over-sensitive to the
far red. Using white light from an inverted incandescent gas
burner of 80 candle power, a marked fluorescence was obtained, the
spectrum of which was easily visible to the eye, and was photographed
by an exposure of ten hours (Fig. 3). It will be seen that the
fluorescence gives two well-marked bands, one about the D line and
the other near the hydrogen red. These bands appear to be related
to the absorption bands of chlorophyll.

The reference lines in the upper spectrum, Figure 1 (taken on

[1] Ber. deut. bot. Gesell., 1888, VI., 1, 36.
[2] Ber. deut. bot. Gesell., 1888, VI., 8, 307.

the same plate), are H red ($\lambda=656$), Na D ($\lambda=589$-590), H green-blue, F ($\lambda=486$), and H blue ($\lambda=434$): from which the phycoerythrin fluorescence bands will be about $\lambda=656$-630 and $\lambda=600$-570.

The absorption bands of chlorophyll differ in position somewhat, according to the solvent used, but in any case these fluorescence bands lie approximately on bands 1 and 3 of chlorophyll, as will be seen from the subjoined table. The values for chlorophyll are those quoted by Czapek.[1]

Chlorophyll Bands.				Phycoerythrin Fluorescence Band.
In Leaf.		In Alcoholic Solution.		
1.=700-654	...	670-635	...	655-630
II.=630-608	...	622-597	...	—
III.=600-578	...	587-565	...	600-570

A still more striking fact is that blue-green light produced the same fluorescence as white light. The blue-green light used was that of the same burner, filtered first through a special shade of green glass, obtained through the courtesy of the London and North Western Railway Signal Department, and then through a purple gelatine. This combination was successful in cutting out all red, orange and yellow light, whilst giving a fair intensity of the blue-green; the spectrum of this light is shown in Fig. 5.

A decided orange fluorescence was visible when a beam of this light was passed through phycoerythrin solution, and the bands in the spectroscope were just visible to the eye. A very long exposure was necessary; 30 hours gave no image, 70 hours only a very weak one, and the photograph shown (Fig. 4), had no less than 210 hours' exposure. The photograph shows a faint band of the blue-green light, no doubt due to reflection from the walls of the glass trough. This was not visible to the eye, nor on the photograph of 70 hours' exposure.

There is thus no doubt that blue-green light does cause the orange fluorescence with bands in the same position as the chlorophyll absorption bands I. and III., and it therefore seems very probable that phycoerythrin does assist assimilation in the manner suggested, *i.e.*, by absorbing the blue-green light and degrading it to yellow and red light of just those wave lengths which can be absorbed by chlorophyll.

II.– CHEMICAL NATURE OF PHYCOERYTHRIN.

It has been suggested by Molisch[2] that phycoerythrin is protein

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[1] Biochemie der Pflanzen, Vol. I., p. 455.
[2] Bot. Zeit., 1894. 52. 177.

in nature. He supports this contention by the following observations on phycoerythrin obtained by crystallisation from aqueous extract of weed.

(*a*.) Phycoerythrin gives the Xanthoproteic reaction.

(*b*). Millon's reagent gave a good result when applied to Phycoerythrin previously bleached by exposure to light.

(*c*). Phycoerythrin is soluble in water only.

On the other hand, Molisch obtained "weak reaction" in the Biuret test.

The facts seem insufficient to establish the protein character of phycoerythrin, and attempts have, therefore, been made to obtain more evidence.

The chief difficulty lies in the purification of the phycoerythrin. It is quite easy to believe that there are protein-like substances in algæ which are extracted by cold water, but is phycoerythrin itself one, or is it a non-protein colouring matter merely carried down in the precipitation of the colloidal bodies?

Experiments were first made to see whether such a dye as eosin was completely precipitated along with egg-white from aqueous solutions. Various proportions of eosin were used, and as eosin is similar in colour and fluorescence to phycoerythrin, approximate matches were obtained to different concentrations of phycoerythrin. The precipitant chosen was alcohol, and it was found that in no case was the whole of the colour precipitated with the egg-white even where the latter was in far greater concentration than any albuminous substance in the algal extract. On the other hand, all the red colour could be precipitated from the Ceramium extract, leaving only a faint dirty-yellow opalescence. This seems to indicate that phycoerythrin is itself colloidal and precipitated by alcohol.

Phycoerythrin also differs from dyes such as eosin in that it is not abstracted from solution by silk.

Estimations of nitrogen have been made, but the results vary. It has been found that the quantity of mineral matter in the crude phycoerythrin, even when using the middle fraction, is always large.

A few figures are given below.

Results on first fraction precipitated (alcohol precipitant).

(*a*). Weight of substance used, 0·0630 gms.

Vol. of N. at 16°C and 771 mm. was 4·4 c.c.

Whence per cent. N. = 8·27.

(b). Weight of substance used, 0·1855 gms.

Vol. of N. at 15°C and 776 mm. was 7·2 c.c.

Whence per cent. N. = 4.65.

The ash in (a) was not determined, owing to lack of substance. (b) contained 17%.

These results probably indicate that the samples (a) and (b), which were made at different times, were mixtures of unlike composition.

Both percentages are too low for true proteins, but the middle fractions give no higher, though more consistent, results.

(c). Weight used 0·172 gms.

Vol. of N. at 17°C and 750 mm. = 5·3 c.c.

Whence per cent. N. = 3·53.

(d). Weight used 0·2594 gms.

Vol. of N. at 12°C and 763 mm. = 7·2 c.c.

Whence per cent. N. = 3·31.

Some of (c) was dried at 100°C to constant weight and 0·1630 gms. lost 0·0248 gms., making per cent. moisture 15·8. Further, 0·1438 gave 0·0390 ash = 27·1%.

Determinations of carbon and hydrogen gave the following results :—

On sample (b) (first fraction) 0·1775, gave 0·2440 gms. CO_2 and 0·1215 gms. of water, or 37·48% C and 7·60% H. On a sample prepared in a similar way to (c) and (d), 0·1862 grms. gave 0.2090 CO_2 and 0·1290 grms. H_2O or 30·61% C, and 7·10% H.

These figures are, however, obtained on material which is probably far from pure, and can only be regarded as provisional.

The action of various reagents on phycoerythrin solution has been studied by Molisch (loc. cit.) and by Schütt (loc. cit.) : these observations have been repeated and extended. The following is a summary of results obtained :—

(1). Phycoerythrin is preciptated from aqueous solution by alcohol, or by saturating the solution with ammonium sulphate or with magnesium sulphate. It is precipitated by very small quantities of mercuric chloride.

(2). Dilute acids, added gradually, first cause disappearance of the orange fluorescence, leaving a lilac-pink tint, somewhat opalescent, and finally, after a couple of days, a pink precipitate settles down.

(3). Ammonia in a small amount removes the fluorescence, leaving a pink colour. Large excess turns this colour to a yellow-brown—similar to that caused by caustic soda.

(4). Caustic soda or potash causes, even in small quantities, a complete disappearance of the rose colour, leaving a yellow-brown very opalescent solution, which, on standing, gives a brownish precipitate.

(5). Sodium bicarbonate and ammonium carbonate produce no effect, even after long standing.

(6). Bleaching powder solution, bromine water and iodine in potassium iodide solution decolorise at once without precipitating.

(7). A saturated solution of mercuric chloride, even in small quantities, produces a lilac-grey precipitate, and leaves an opalescent pinkish solution, which, after further addition of mercuric chloride solution and standing, gives a further dull grey precipitate, leaving a nearly clear slightly yellowish solution.

An analysis of the first precipitate gave :—

Weight of precipitate taken = 0·1663 gms.
Vol. of N. at 17°C and 775 mm. was 6·6 c.c.
Whence per cent. N. = 4·7.

The precipitate gave qualitative reactions for mercury and chloride.

(8). Ferric chloride solution gave a pinkish-brown precipitate.

(9). Concentrated nitric acid, on boiling, gave a yellow colour deepened to orange by addition of excess of ammonia.

(10). Millon's reagent, on boiling, gave a deep red colour.

(11). Caustic soda solution, followed by a drop of dilute copper sulphate solution, did not give either a violet or a pink colour, but a slight greenish tint.

(12). It is not abstracted from its aqueous solution by silk.

ACTION OF PROTEOLYTIC FERMENTS ON SOLUTION.

(a). PEPSIN.—0·1 gm. pepsin and I c.c. of "twice normal" hydrochloric acid were added to 50 c.c. phycoerythrin solution containing a trace of eucalyptus oil as antiseptic. A similar check experiment was performed using 50 c.c. of milk, also containing eucalyptus oil. The tubes were maintained at a temperature of 33° to 38°C in a water bath for forty-eight hours, but no change occurred in the phycoerythrin, whilst the casein in the milk (precipitated on adding the acid) had largely disappeared.

Another sample of the same pepsin (0·2 gms.) in 40 c c. two per cent hydrochloric acid completely dissolved 0·2 gm. of hard-boiled white of egg in half-an-hour.

(b.) TRYPSIN.—0·2 gms. sodium bicarbonate and 2 c.c. Lotio Pancreatis (Fairchild) were added to 50 c.c. phycoerythrin solution and a similar quantity of each to 50 c.c. milk and 10 c.c. of water. These tubes were kept at 33°—38° for forty-eight hours and tested

from time to time. A trace of eucalyptus oil was added to each as antiseptic.

The milk after eight hours gave no coagulation on adding dilute acid, and with the Biuret test gave a rose colour instead of the violet given by fresh milk.

The phycoerythrin lost its colour and gave finally a practically colourless, slightly opalescent, solution.

This solution was evaporated to a sirup and examined microscopically for tyrosin and leucin. No tyrosin could be found, but there appeared to be a very little leucin. The amount of phycoerythrin in 50 c.c. of solution is, however, very small (two litres give about ·5gms. of crude phycoerythrin), so that the amount of hydrolysed products could not be great.

HYDROLYSIS BY ACIDS.—·5 gms. of solid phycoerythrin (middle fraction) was boiled for twenty-four hours with 50 c.c. dilute sulphuric acid (one vol. conc. H_2SO_4 to nine vols. water), the solution filtered from a small residue, neutralised with barium carbonate and again filtered. The filtrate and washings were concentrated to a sirup.

The residue on examination under the microscope gave no signs of tyrosin, but a good amount of characteristic leucin crystals. Chemical tests gave slight reactions for tyrosin, but confirmed the idea that leucin was in far the greater amount.

CONCLUSIONS.

The above results appear to show :—

(1). That phycoerythrin plays the part of assistant to chlorophyll by absorbing blue-green light and degrading it to the light which corresponds to the absorption bands I. and III. of chlorophyll.

(2). That phycoerythrin is probably a colloidal nitrogenous substance, related to protein—but not a true protein, as its nitrogen content is too low and it does not give the Biuret reaction. The evidence is incomplete; pure phycoerythrin has still to be prepared and even comparatively pure phycoerythrin in sufficient quantity for extended chemical investigation has not yet been obtained.
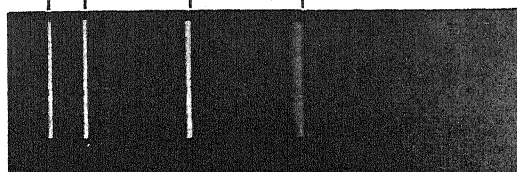
$\lambda =$ 656 589   486   434

1
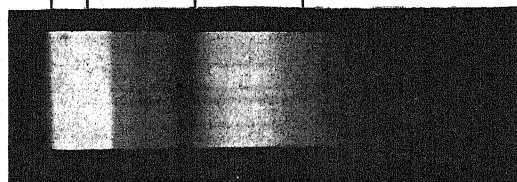
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3

4

5

656 589   486   434

HANSON—PHYCOERYTHRIN.
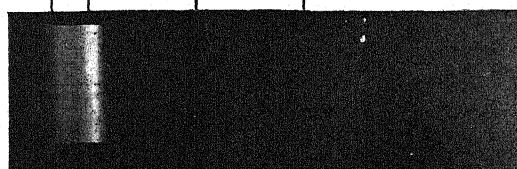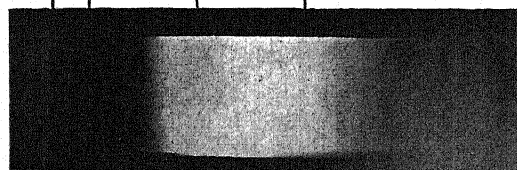
THE EMBRYO-SAC AND EMBRYO OF *GEISSOLOMA MARGINATA.*

By E. L. Stephens,

(Newnham College, Cambridge),

[Plate VI.]

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*G*EISSOLOMA MARGINATA is a small shrub, of an ericoid habit, confined to the South-West region of South Africa, and of very rare occurrence within that region. Material for the present investigation was obtained from a small patch growing on Garcia's Pass in the Langeberge Mountains, in the south of Cape Colony, during a vacation botanical expedition from the South African College, Cape Town,

The systematic position of this plant has been disputed, but it is usually regarded either as an anomalous genus of the Penæaceæ[1] or as the sole representative of a separate order—the Geissoloma-ceæ[2] or Geissolomataceæ[3]. The present investigation was under-taken to see whether the structure of its embryo-sac resembled in any way that found in the former order.

A single sporogenous cell is differentiated in the young ovule, but as no satisfactory preparations of the stages in its division have been obtained, it cannot be said whether or not the usual row of megaspores is formed. There is, however, strong presumptive evidence that it does occur. Thus, in Fig. 1, which shows the youngest stage of the embryo-sac seen, the developing megaspore is crowned by a deeply-staining mass which probably represents the remains of the megaspore row, and a similar appearance has been seen in several other preparations at the same stage. More-over, the appearance of the first four nuclei formed in the embryo sac (Figs. 1—3), suggests that they are the results of ordinary nuclear divisions, and not of meiosis.

The eight-nucleate is reached in the usual manner (Figs. 1—4). As soon as the eight nuclei are formed they begin to show differences in size and staining properties, and this differentiation rapidly becomes very marked. The upper polar nucleus at once

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[1] Bentham and Hooker. Genera Plantarum III. London, 1880. p. 203.

[2] Sonder, W. Beiträge zur Flora von Sudafrica. Linnæa, XXIII. (Halle, 1850), p. 105.

De Candolle. Prodromus XIV. Paris, 1856, p. 491.

[3] Engler. Syllabus der Pflanzenfamilien. Berlin, 1909, p. 177.

moves to the lower end of the sac to fuse with the lower one (Figs. 4 and 5); in several cases the nuclei were found to have completely fused before fertilisation (Fig. 8). The three antipodal nuclei decrease in size and quickly lose their staining properties. Ill-defined cells are formed around them (Fig. 5), completely filling the narrow lower end of the embryo-sac, and whilst the rest of the sac grows rapidly, this end remains small. It consequently can be recognised, at a slightly later stage, only as a small pocket at the antipodal end of the sac; while as the sac increases still more in size, at the expense of the antipodal nucellar tissue, it disappears along with this tissue (Fig. 6A). Even before this happens, the nuclei have degenerated, so that they are rarely recognisable at later stages than that of Fig. 5. The antipodal cells thus apparently take no part in the activities of the embryo-sac. The egg-apparatus is of the usual type. The nuclei of the synergids, with the surrounding protoplasm, take up stains very deeply, each synergid thus usually forming a deeply-staining mass with a small clear apical portion (Figs. 5, 6A).

The nucellus is composed of a central strand of elongated cells surrounded by starch-filled parenchyma. The embryo-sac, elongating laterally downwards, digests this parenchyma, and simultaneously large grains of starch begin to appear in the proto-plasmic layer lining the sac (Figs. 5, 6A). These grains again begin to disappear as the embryo-sac attains its maximum development before fertilisation and the starch-bearing tissue becomes used up (Fig. 7).

A copious endosperm is formed after fertilisation, filling up the embryo-sac. It is only partly resorbed by the developing embryo, which lies in a sap-containing cavity closely surrounded by it (Figs. 9—11).

As in the Penæaceæ, there is no suspensor. The pro-embryo is at first pear-shaped (Fig. 9), but later becomes spherical (Fig. 10), the whole of it entering into the composition of the embryo. The cotyledons, which are long and linear, become differentiated at a much earlier stage (Fig. 11), and are much better developed than is the case in the Penæaceæ.

The chief point of interest in connection with the embryology of this plant lies in a comparison with the closely allied Penæaceæ, there having been some discussion[1] as to whether the peculiar type

[1] *see* Stephens, E. L. The Embryo-Sac and Embryo of certain Penæaceæ. Ann. Bot., 1909, XXIII., p. 363—378.

1   2   3   4   p.n.   5

e.s.   6   6ª   p.n.   7ª   end.

8   p.n.   7   II

end.   9   end.   10
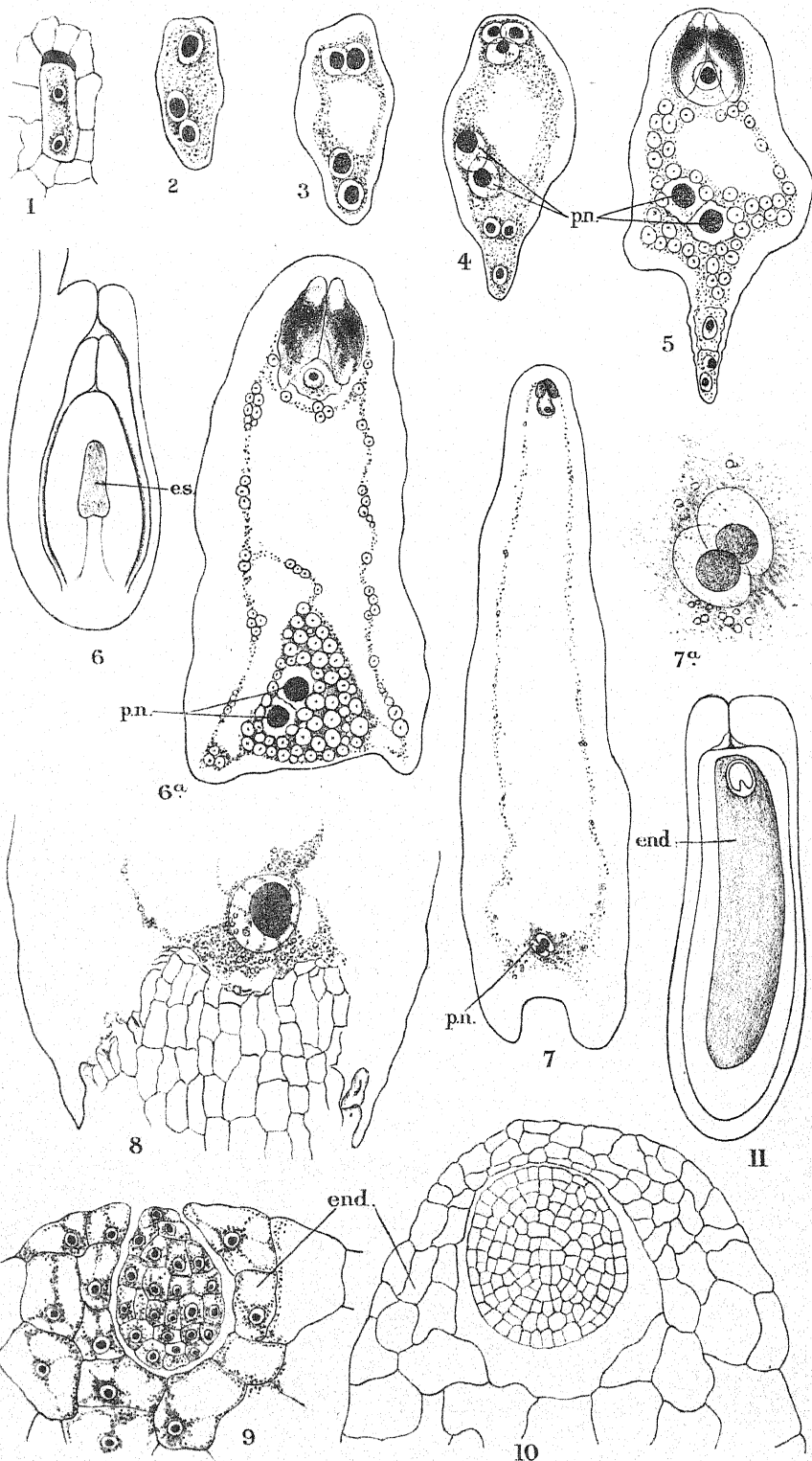
of embryo-sac found in that order can be considered as more primitive than the normal Angiospermous type, or as derived from it. In the Penæaceæ, both the structure of the embryo, apparently highly adapted to xerophytic conditions,[1] and the comparatively feeble development of the endosperm, probably point to a higher degree of specialisation than is the case in *Geissoloma*. The embryo-sac of the Penæaceæ then might be expected to show a correspondingly higher degree of development. As the embryo-sac of *Geissoloma* is, if anything, rather specialised from the normal type (as is shown by the marked differentiation in the egg-apparatus, and the evanescence of the antipodals), it may be inferred that the Penæaceæ probably show a still further specialisation. Thus the evidence derived from the study of this form supports the conclusion that in the embryo-sac of the Penæaceæ we have, not a relatively primitive type, but rather one which is derived from the normal by the inclusion of four megaspores in its development.

SUMMARY.

Geissoloma marginata is the only representative of the order Geissolomaceæ, which is closely allied to Penæaceæ. The embryo-sac is probably derived from one of a row of megaspores. Its development is that of a typical Angiosperm, but the antipodal cells are very evanescent. It contains much starch. The pro-embryo is at first pear-shaped, later spherical, with no suspensor. The embryo lies in a copious endosperm.

The fact that this close ally of the Penæaceæ has a normal embryo-sac tends to uphold the view that *Geissoloma* is to be regarded as a representative of a separate order rather than as an anomalous genus of the Penæaceæ.

This investigation has been carried out in the Cambridge Botany School, by kind permission of Professor Seward.

[1] Stephens, E. L. *loc. cit.*, p. 369.

EXPLANATION OF PLATE

ILLUSTRATING MISS STEPHENS' PAPER ON THE EMBRYO-SAC AND EMBRYO
OF *GEISSOLOMA MARGINATA.*

Fig. 1. Binucleate embryo-sac; the disintegrating mass above may represent the remains of the other megaspores. × 430.

Fig. 2. Three nucleate embryo-sac. × 430.

Fig. 3. Four nucleate embryo-sac. × 430.

Fig. 4.   Eight nucleate embryo-sac.   × 430.

Fig. 5.   Later stage ; the sac has begun to broaden near the base and starch
has appeared in it.   × 430.

Fig. 6.   Longitudinal section through an ovule at a stage later than Fig. 5,
showing the growing embryo-sac.   × 66.

Fig. 6A.   Embryo-sac of Fig. 6.   × 430.

Fig. 7.   Mature embryo-sac, showing axial cone of nucellar cells projecting
into the base ; much of the starch has disappeared.   × 172.

Fig. 7A.   Polar nuclei of Fig. 7.   × 860.

Fig. 8.   Base of another mature embryo sac, showing definitive nucleus. × 430.

Fig. 9.   Young embryo.   × 280.

Fig. 10.   Later stage ; the embryo-lies in a sap-containing cavity surrounded
by endosperm × 280.

Fig. 11.   Longitudinal section through ovule at a later stage than Fig. 10,
showing endosperm, and embryo with developing cotyledons,
× 15.

NOTES ON *POLYPORUS SQUAMOSUS*, HUDS.

By F. T. Brooks, M.A.

(Demonstrator of Botany, University of Cambridge).

[Text-Fig. 44.]

THE following notes were made last summer in regard to some
sporophores of *Polyporus squamosus* which developed under
conditions particularly favourable for observation.   In regard to
the liberation of spores, these remarks are confirmatory of Buller's
extensive work[1] (reviewed in the present issue) on this portion of
the general biology of certain groups of the Hymenomycetes.

A cylindrical block of *Acer Negundo* about a foot in diameter had
been brought into a room during the early part of May for the use
of the Department of Forestry at Cambridge.   On May 18th two
groups of fungus fructifications which evidently belonged to *Poly-
porus squamosus* were seen to be arising from the bark.   When
enquiries were made at the Botanic Gardens whence the block had
come I learnt that the specimen had been cut from a tree which
had been attacked *in situ* by this fungus.   One group of fructi-
fications consisted of a bulbous base from which three stalked
sporophores of different sizes arose, the other comprised a similarly
swollen base and a single rudimentary pileus.   During the three
weeks that the fructifications were kept under observation the

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[1] Buller, A. H. R.   "Researches on Fungi," Longman & Co.,
1909.

block of wood remained in a constant position in a dimly lighted
room; the larger group of sporophores faced the window, while the
smaller one was on the opposite and darker side of the block.
Throughout the course of the observations the single sporophore
which was on the side of the wood remote from the light remained
in a rudimentary condition. This is to be accounted for presumably
by the diversion of the stream of nutritive material derived by the
sterile mycelium in the wood, to the other group of sporophores
which were further advanced in development. It is not likely that
diminished light on that side caused a cessation of further growth,
because Buller has shewn[1] that as long as feeble light is allowed to
impinge upon the sporophore for a short time when young, the
fructification will then develop normally although kept in complete
darkness.

The dimensions of two of the sporophores of the larger group
of fructifications were taken daily by measuring the two longest
axes of each at right angles to one another. The third sporophore
of this group grew for a short time and then its development ceased,
doubtless on account of the available food material being used by
the larger pilei. The temperature of the room in which the obser-
vations were made varied between 7·8°C and 17·3°C. The following
table indicates the amount of linear growth which occurred in the
two pilei—called A and B, during the period of observation. On
May 23rd and 24th respectively the pilei ceased to increase in area.

PILEUS A.

				Length of Axis I.		Length of Axis II.
May 10th	...	...	...	5·8 cm.	...	8·1 cm.
May 23rd	...	...	...	18·3 cm.	...	27·5 cm.
Growth during 13 days		...		12·5 cm.	...	19·4 cm.

PILEUS B.

				Length of Axis I.		Length of Axis II.
May 10th	...	...	...	3·6 cm.	...	4·7 cm.
May 24th	...	...	...	13·1 cm.	...	18·7 cm.
Growth during 14 days		...		9·5 cm.	...	14·0 cm.

These figures indicate the rapidity with which the fructification
of this fungus grows. The daily measurements are being examined,
and it is hoped that they will throw some light on the manner in
which growth takes place in the sporophore of *Polyporus squamosus.*

[1] Buller, A. H. R. Loc. cit., p. 59.

It may be pointed out here that an appreciable falling off in growth was observed during the daytime.

On May 23rd, *i.e.*, about the time when growth ceased, spores began to collect upon a piece of black paper placed below the fructifications.   No deposition of spores in quantity occurred before this date,   On closer examination, the spore cloud already described by Buller[1] as being discharged from *Polyporus squamosus* could be seen distinctly.   This faint cloud may be compared with the smoke arising from a smouldering tobacco pipe.   The discharge of spores in this manner continued without interruption for a period of ten days.   Buller mentions one case in which the spore cloud was emitted for sixteen days.   The floor in the vicinity of the block of wood became white with spores.   An idea of the enormous quantity of spores produced can be gathered from the accompanying photograph (Text-fig. 44).
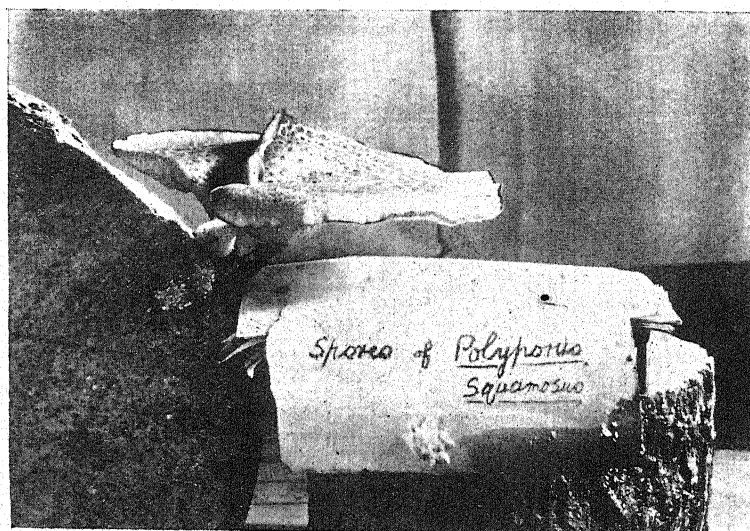
Text-fig. 44. " Spore-cloud " of *Polyporus squamosus*. Below the sporophore was placed a piece of black paper, which, together with the surrounding objects, became covered with a thick layer of spores.   The paper was so thickly coated that it was possible to write an inscription in the spore covering.

Another interesting phenomenon exhibited by these fructifications was the production of drops of liquid on the under surface. It was noted that these drops formed only towards the end of the period of growth in area of the pileus and after such growth had ceased. This exudation of water is presumably analagous to that

[1] Buller, A. H. R, Loc. cit., p. 89,

which takes place through the hydathodes of the higher plants. The sporophores of other Polyporeæ often liberate drops of fluid from their hymenial surface and in the case of *Polyporus hispidus* considerable quantities of liquid are known to drip away in this manner. The exudation of water from the hyphæ of other fungi is of common occurrence. One may recall the case of *Pilobolus crystallinus*, on the sporangiophores of which drops of liquid are frequently seen.

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HYBRIDS BETWEEN *GALIUM VERUM* & *G. MOLLUGO.*

BY ELEONORA ARMITAGE.

[TEXT-FIG. 45.]

THE following notes describe three distinct forms of Galium hybrids which I found this year in Herefordshire growing with their parents, *G. verum* L. and *G. Mollugo* L. The forms B and C I had found before, but A was new to me. Tables and figures are added to give a rapid comparative view. The drawings, measurements and notes were made from the fresh material. In describing the leaf-whorls, the usual systematic designation of "leaves," without differentiating leaves and stipules, is retained. The descriptions are taken from the whorls of leaves on the primary stems, not the branches; and as the leaves vary in size according to their position on the stem, becoming smaller upwards, the measurements have been taken from medium leaves in the middle of the stem, all thus pointing to a mean. The two species are first described, as affording the greatest contrasts.

No. 1. *Galium verum* L. The stem of this plant has four obscure angles. The leaves are narrowly linear with a sharp point, margin inrolled; the upper surface slightly rugose, and with small prickles, but appearing smooth and shining to the naked eye. There is a row of larger, forward-pointing prickles on the *apparent edge* of the leaf, not on the *margin*, where, as the latter is inrolled, they would be useless. As the leaves are bent back downwards to the stem, the prickles function as reflexed and act as holdfasts. The leaves are 7 to 8 in a whorl, 18 mm. long. The bright

yellow flowers are borne on narrow branched panicles, a medium branch being 4 cm. long. The corolla has four broad lobes, very shortly pointed, the lobes patent or directed slightly forward. The flowers in all forms are proterandrous; the gynæceum is bilocular with one ovule in each loculus, and in this species the ovules in each cell were fertile.

No. 5. *Galium Mollugo* L. The stem has four marked wings. The leaves are about 6 in a whorl, short, 12 mm., broadly oblong, mucronate, surface flat, shining, with forward prickles on the *margin.* The large long-branched panicle has its middle branches about 20 cm. long; the corolla has four oblong lobes with prolonged pointed apices, reflexed, pure white; both cells of the ovary are usually fertile, but one is sometimes aborted.

Of the three hybrids, A most nearly resembles *G. verum;* C most nearly resembles *G. Mollugo;* while B is just intermediate between the two species.

No. 2. Hybrid A. Stem with four obscure angles; leaves 7 to 9 in a whorl, linear, inrolled, rather longer than those of *G. verum* (24 mm.), broader, with forward prickles on the *edge,* upper surface dull and rugose, with prickles. Panicle rather larger and more
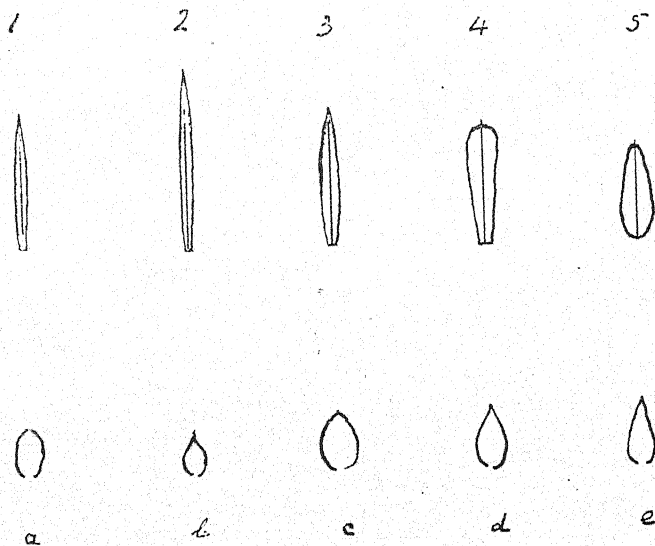
TEXT-FIG. 45.

1.	Leaf of *G. verum.*	*a.*	Corolla-lobe of *G. verum.*
2.	,, Hybrid A.	*b.*	,, ,, Hybrid A.
3.	,, ,, B.	*c.*	,, ,, ,, B.
4.	,, ,, C.	*d.*	,, ,, ,, C.
5.	,, *G. Mullugo.*	*e.*	,, ,, *G. Mollugo.*

branched than that of *G. verum*; medium branch 8 cm. long; corolla with four broad lobes, more distinctly mucronate, slightly reflexed, colour deep lemon-yellow.

No. 3. Hybrid B. Stem with obscure angles; leaves 7 in a whorl, narrowly lanceolate, pointed; margins very slightly inrolled, with prickles on *edge*; upper surface slightly shining, with small scattered prickles, 14 mm. long. Panicle longer and broader, medium branch 14 cm. long. Corolla with oblong shortly-pointed lobes, pale buff or cream colour.

No. 4. Hybrid C. Stem with marked angles or wings. Leaves about 6 in a whorl, short, 15 mm., broadly oblanceolate, mucronate; flat, with forward prickles on margin, upper surface smooth. Panicle much larger and laxer, medium branch 20 cm. long; corolla lobes oblong with prolonged apices, cream-coloured, the flowers smaller than those of *G. Mollugo*.

TABLE I.—VEGETATIVE CHARACTERS.

Plant.	1	2	3	4	5
Character.	*G. verum*.	Hybrid A.	Hybrid B.	Hybrid C.	*G. Mollugo*.
Stem angles...	obscure	obscure	obscure	winged	winged
Leaves ...	linear	linear	lanceolate	oblanceolate	oblong
Leaf margin	inrolled	inrolled	slightly rolled	flat	flat
Leaf length mm.	18	24	14	15	12
Leaf apex ...	pointed	pointed	pointed	mucronate	mucronate

TABLE II.—FLORAL CHARACTERS.

Plant.	1	2	3	4	5
Character.	*G. verum*.	Hybrid A.	Hybrid B.	Hybrid C.	*G. Mollugo*.
Panicle branch length mm.	4	8	14	20	20
Corolla lobe...	broad	broad	oblong, smaller than 5	oblong, smaller than 5	oblong
Apex of lobe...	short point	mucronate	short point	prolonged	prolonged
Corolla colour	bright yellow	lemon yellow	buff cream	cream	white

BOTRYCHIUM LUNARIA WITH TWO FERTILE LOBES.

Text-Fig. 46.
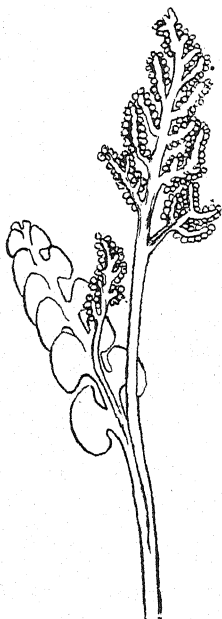
[TEXT-FIG. 46.]

THIS summer on one of the old moraines at Arolla, Canton Valais, Switzerland, I found a specimen of *Botrychium lunaria* with duplicate fertile lobes on the frond (Text-fig. 46).

As far as I know such a specimen has not been recorded before, although it is not uncommon for the usually sterile part of the frond to bear sporangia. The present shoot is analagous with the normal condition of *Ophiog. palmatum* and seemed worthy of record owing to the limited and isolated character of family.

M. BENSON.

VEGETATION AND FROST.

> Ah, bitter chill it was!
> The owl, for all his feathers was a-cold;
> The hare limp'd trembling through the frozen grass;
> And silent was the flock in woolly fold:

THE contrast between the effects of external cold upon the two kingdoms of living things suggested in this shivering picture is a characteristic one. The animal suffers the sensation of cold, but protects itself from actually freezing by greater heat-producing metabolism, within non-conducting coverings; while the plant, which has no such adaptations, cools down *pari passu* with the environment, and freezes solid.

In our comfortable conviction that the plant, in so doing, suffers no agony of cold we may reserve our sympathies for our nearer brethren, but it will be a not unseasonable enquiry to consider in a general way the relation of plant-vitality to such low temperatures as occur normally in the winter months.

I propose in this article, therefore, to give some account of the present state of our knowledge on this matter, which was materially advanced, not long ago, by the publication of the detailed results of Lidforss' investigations on the plants that remain green through the winter (the "winter-green" flora) in South Sweden.

A critical account of the earlier literature upon the subject does not come within the scope of this article and we will begin with the pamphlet published by Molisch a dozen years ago and then pass to the work of Mez, 1905; Gorke, 1906; and Lidforss, 1907. The various works by Muller-Thurgau on this subject are of great importance, but published in 1880, 1882 and 1886, they are hardly recent enough for detailed notice.

The well established fact that Yeast, Bacteria, and some moulds can withstand prolonged exposure to the cold of liquid hydrogen, teaches us that there is no primary essential injurious effect in chilling protoplasm.

Nevertheless most sappy parts of the higher plants are killed by cooling much below 0°C. We have to enquire what this injurious indirect effect of cold may be and why some plants are so much more resistant than others. One general secondary effect of cold is the formation of ice within the tissues of the plant, and another is alteration of the balance of the chemical changes that are going on in the cells. As a tertiary effect we have the dessication that results on withdrawing water as solid ice and this again might give rise to a quaternary class of effects due to the very concentrated solutions of the cell-constituents in which the protoplasm would be bathed in a partly frozen cell.

To Molisch we owe the first direct observations, with microscope and freezing mixture, of the formation of ice in plants. He noticed that in the living plant ice-formation does not always take place immediately the temperature has fallen to the freezing point of the sap, which of course is below zero just in proportion to the amount of dissolved substances in it. Indeed he found a good parallel with the phenomena observed on freezing salt-solutions in general. Thus just as drops of water suspended in olive oil may be over-cooled many degrees below zero without ice-formation, till suddenly they solidify completely and the temperature rises to the true freezing point of water, so the hairs of *Tradescantia* stamens may be cooled to —6·5°C and then suddenly the cells fill with crystals of ice. Further as water in a fine capillary tube ·3 mm. diameter

resists freezing till it has been over-cooled to —10°C so the capillary mycelium of *Phycomyces* may, in air, be cooled to —17°C before ice is formed in it.

It is exceptional for ice to form inside cells, and on cooling cells mounted in water, the outside water freezes first and then water is gradually withdrawn from within the cell to form more ice on the outside of the cell-wall. A filament of *Spirogyra* when frozen in this way is so shrunken, that under the microscope it looks exactly like a shrivelled dried-up thread. When tissues of higher plants are frozen, films of pure ice form on the walls abutting on intercellular spaces, and these films grow steadily to quite large lumps of ice causing disruption of the tissues.

Muller–Thurgau and Molisch held that the fatal effect of this freezing should be traced to the resulting dessication of the protoplasm whereby its structure was irrecoverably disorganised. As long as the ice-formation is staved off in sappy plants the cold does not kill. For sudden death on cooling ice-formation is essential, whether it acts as Molisch suggests straight upon the protoplasm, or only indirectly. The reverse is, of course, not at all true, as many plants recover readily after being frozen solid.

Dominant by the authority of Sachs the erroneous view had long been held that it is only on the thawing of the cell that the fatal disorganisation sets in, and that if thawing proceeds very slowly recovery may take place which would not be attained with quick thawing. Molisch has ingeniously and finally demonstrated the complete incorrectness of these views. He cooled the red marine Alga *Nitophyllum* to —5°C when it froze and on keeping it frozen the brilliant orange red fluorescence of the phycoerythrin in the cell soon became very obvious. In the living cell the pigment exhibits no fluorescence and this appearance is a sure sign of death. By similar treatment of the leaves of *Ageratum mexicanum* the odour of coumarin was soon developed, without any thawing having taken place, and this odour, which results from *post-mortem* ferment action within the cell, is also evidence of the death of the cell.

Definite experiments made with a number of plants showed that only in one exceptional case, *Agave*, did the rate of thawing make any difference to the question of death or recovery.

In 1905, Mez developed a different point of view. He thinks that death by " cold-dessication " is only exceptional, perhaps true only for water-plants and holds that protoplasm is directly susceptible

to cold and that there is for each cell a fatal "*minimum*" temperature. Further, for plants which can stand the formation of ice in their tissues he thinks it is an advantage that in a cold environment (he worked with —14·5⁰C experimentally) the ice should form as quickly as possible. The protective action of the ice lies in this, that conduction away of the plant-heat is not half as quick in solid ice as it is in a liquid or watery tissue. Consequently the inner parts are much longer in cooling to their fatal minimum.

The formation of ice from sap in tissues leads to the liberation of the latent heat of the water and crystallising out of sugar from the sap would also generate heat. If these radiations were adequately isolated by non-conductors from the outside cold, the delay in cooling down to the minimum might be very considerable. Mez holds that the storing-up of sugars in the periderm of trees and in evergreen leaves (cf. Lidforss) is a preparation of substances which will give out a little protective warmth when concentrated to crystallisation by ice-formation. It is clear that these principles must be at work in the plant, but it is difficult to determine the magnitude of their biological significance.

Mez shows clearly that when a sappy piece of tissue (he used largely the nodes of stems of *Impatiens*) is cooled down and its internal temperature registered by an imbedded thermo-junction it goes through the same phases as a solution of its constituent substances would. The falling temperature on cooling passes through a phase of separation of pure ice into a phase where the solutes have become so concentrated that they and the ice crystallise out at an equal rate. During this phase the temperature remains constant and only when it is over and the whole mass is frozen solid does the temperature once more fall.

According to Mez this freezing temperature was never observed to be below —6⁰C, so that in time "cold-dessication" should be *complete* at this temperature and the protoplasm should not suffer any more by further cooling, on the hypothesis that all the injury is simply due to dessication. This clearly goes against the view of Muller-Thurgau and Molisch, and we shall see in the work of Gorke that there are other ways in which withdrawal of water may injure the protoplasm besides direct dessication.

In 1906, Gorke made experiments on changes in composition produced by freezing, either whole plants or their expressed sap, which brought to light a quite new factor. It is well known that

the natural proteids can, by the addition of concentrated neutral salts to solutions of them, be " salted out " as precipitates, which at first can be redissolved on dilution but on standing become insoluble and "denatured." It occurred to Gorke that when the plant is frozen and water is withdrawn from the cell, the salts present must become more concentrated and might well in time act on the soluble proteids of the cell and cause their precipitation. This expectation was realised and he found that barley which has been put out at —7ºC for a night and been frozen solid, yields, on expression of its sap after thawing, a juice which contains only 2/3 of the amount of proteid in solution which the expressed sap of the unfrozen control culture of barley yielded.

He went further and showed that the low temperature required to precipitate proteid from the expressed sap of different *normal* plants varied considerably; that it was mild in the case of those plants that suffered severely from cold, but that a very low temper-ature was required in the case of very resistant plants. Thus the freshly expressed sap of *Begonia* or *Pelargonium* (which are easily injured at —5ºC) yields a denatured precipitate of proteid at —3ºC, in time, while winter-rye is only precipitated at —15ºC and the sap of Pine needles not until —40ºC. The production of this effect will of course vary with the nature of the proteids present and also with the nature and amount of the salts present in addition. Gorke made up solutions of egg-albumin with mixtures of salts like those in the cell and found that after freezing to — 20ºC there was a large and permanent precipitate. All this work deals with the soluble proteids of the cell, but one may reasonably transfer the idea to the structural proteids of protoplasm to account for the killing effect.

It had been previously observed that on lowering the temperature of solutions of certain acids like tribasic phosphoric acid, the acidity slightly increases, so that more alkali is required to neutralise it, and that therefore a mixture with alkali, neutral at ordinary temperatures, would develop acidity on cooling. Gorke found that the sap of plants also shows an increased acidity on cooling, which would of course help in precipitation and denaturation of proteids at low temperatures.

We will now pass to Lidforss' work on his Swedish winter-green flora. The plants which in mid-winter are to be found still bearing green leaves belong to a variety of ecological types. None of these appears to show any obvious adaptation for protection from winter

cold, and perhaps the most interesting are those delicate herbaceous annuals which look so unfitted for winter existence—*Holosteum, Cerastium, Lamium, Veronica, Senecio, Viola, Fumaria,* etc. Even in the Arctic flora there is nothing protective to compete with the snug coatings of our feathered, furred and fleecy friends and Kjellman concluded that protection from injury by frost must lie in the nature of the protoplasm.

Lidforss has, however, established one general characteristic of all these plants in winter-time which does seem clearly to be protective. He finds that all winter-green leaves are quite free from starch but contain quantities of sugar (and sometimes oil) in the mesophyll. In the summer these same leaves contain abundant starch. This they regenerate in spring and if the plants are brought from the open into a warm room in mid-winter, starch is also usually soon regenerated from the sugar.

The only exceptions which Lidforss found were the submerged water-plants like *Elodea, Chara,* which show starch all through the winter. The rule obviously does not break down on proof by the exception, for submerged plants are in an environment which will not fall below zero.

Few of these winter-plants belong to Stahl's saccharophyllous class characterised by general absence of starch-formation, low transpiration rates and tolerance of dry soil, which lowness of transpiration is held to be a direct result of the high sugar-content of the evaporating sap of the mesophyll cells. In winter all soil is physiologically dry and the sugar might help to keep down the transpiration and avoid the evils of wilting, but Lidforss finds a much more direct advantage in its presence.

He first demonstrated that the sugar in the cells does enable them to survive a lower temperature. This can be proved by the simple preliminary treatment of keeping cut leaves with their stalks in sugar solution (5-10% of any ordinary sugar) for a few days. *Nerium* and *Viburnum Tinus* are particularly good at taking up sugar in this way without becoming at all wilted.

When these sugared leaves are exposed to a frost of —7⁰C they remain uninjured, while controls that had been kept preliminarily alongside them in water are killed and show this by turning quickly brown by *post-mortem* oxidative changes.

Most leaves exhibit this protective action of sugar more or less, the real difficulty is to get the sugar into the mesophyll cells

Not only leaves but seedlings of *Helianthus,* and roots of *Vicia*

can be protected by intake of sugar. The last named material after 18 hours in 5% levulose survived four hours, frozen at —2°C, while roots without sugar were all killed.

Water plants fall into two sharply marked classes in this connection. *Elodea*, *Chara*, and *Stratiotes*, which in winter vegetate at the bottom of streams at a temperature just above zero, contain starch but no sugar and are killed on exposure to —2°C or —4°C. In contrast to these we find at the edge of the stream the submerged wintering stumps of the plants which vegetated above the water in the summer, such as *Menyanthes*, *Ranunculus lingua*, *Myosotis*, *Sium*. These have all converted their starch to sugar for the winter and in correlation it is found that a temperature of —7°C is required to kill them.

Another phenomenon which seems to be explained by Lidforss' work is the puzzling fact that many a plant which has survived the profound and prolonged cold of winter may be killed by a sharp night-frost in early spring (long before, of course, it has started any new growth). This is especially common when the night-frost is preceded by a spell of bright sunny radiation. The accepted explanation is that it is the quick change of temperature from warm day to cold night that injures, but all experimenters agree now that the rate of cooling or thawing makes very little difference. Lidforss finds that a succession of warm days in spring causes the regeneration of starch and holds that it is the disappearance of the protective sugar that makes the plant more susceptible. This is borne out by his observations that it is the well-sunned south side of trees like *Ilex* and *Taxus* that suffer in such weather and that here the sugar has gone, while the shaded north side of the tree still keeps its sugar and is uninjured by the spring frost.

In *Holosteum umbellatum* a warm January day with a temperature of +5°C starts the regeneration of starch and if a cold spell follows, it may revert to sugar.

Warming up a leaf in a greenhouse for a week when, as sometimes happens in the early winter, it can be done without an appreciable fall in the sugar content, does not make the leaf more susceptible to cold, so that clearly it is not the direct effect of warmth that matters.

In South Sweden the starch of vegetation gives place to sugar, rather quickly, in November, and remains thus till early or middle April when the reverse change takes place, but there the winter is more prolonged than in our climate.

This brings us to Lidforss' theory of the protective action of sugar. It is simply this, that the presence of sugar retards the salting-out effect investigated by Gorke. Spiro had found that the presence of non-electrolytes, like alcohol, glycerine, sugars, etc., hinders the coagulation of proteids, and that indeed the presence of sugar may raise the heat-coagulation point of a given proteid from 59°C to 85°C.

Lidforss found by experiment that the addition of 5% to a mixture of egg-albumen and dilute Knop's nutritive salt-solution much diminished the amount of proteid precipitate that ensued on freezing, and that 10% sugar prevented altogether such precipitation.

Combining this with Gorke's experiments on freezing whole plants and actual expressed sap, it seems safe to transfer these effects observed *in vitro* to the living cell, and to accept this theory that the universal formation of sugar in winter-leaves acts as a distinct protection against winter cold.

To prevent our deriving too great satisfaction from this interesting chain of reasoning, we may recall that two characteristic sugar-plants, the sugar-cane and the sugar-beet are both very susceptible to cold and that sugarless Bacteria on the contrary are very resistant. Of course the constitution or composition of the protoplasm will have the final word in this matter.

We may now attempt to carry our enquiry a stage further and ask how it comes about that winter-leaves convert their starch to sugar.

This phenomenon is not confined to leaves, but Russow and Fischer found that in most trees the periderm of the trunk contains sugar and oil in winter, in place of the starch present in summer.

Potato tubers too kept at temperatures near zero are well known to turn sweet and unpalatable. This interesting phenomenon was worked at with great insight and precision by Muller-Thurgau as long ago as 1882. He first shewed that sugar formation was not the result of injury by frost and that indeed it does not take place when the tuber is kept frozen hard, below —1°C. At 0°C the conversion of starch to sugar proceeds steadily, and potatoes stored upon ice may go on accumulating sugar for forty or fifty days. The accumulation begins slowly, and then proceeds faster and faster for a time, till it reaches somewhere about 3% of the fresh weight. Then the increase stops and the sugar content is

maintained at about that amount. This we should consider as the result of the accumulation of the products of diastatic hydrolysis of starch hindering the further progress of the reaction (to speak statically). That the limit attained depends on the concentration of the sugar Muller showed by cooling potatoes which had been caused first to lose a lot of water by slow drying. These potatoes formed sugar to about the same concentration, and therefore to a less absolute amount than watery turgid tubers.

If potatoes are hept at $+3^0$ the sugar content does not rise above ·5%, while at $+6^0$C hardly a trace of sugar is to be found. This phenomenon is then essentially a disturbance of metabolic balance due to low temperature. The amount of sugar at any moment depends partly on the diastatic activity and partly on the consumption of the sugar in respiration. As the temperature falls, the respiration will be much diminished, and this favours the accumulation of sugar. Diastatic activity is also diminished by cold, but the equilibrium point finally attained between starch and sugar is shifted towards the sugar by cold. Equilibrium points of reversible reactions are always shifted with fall of temperature in the direction of a greater concentration of the products of the exothermic direction of the reaction ; that is, in this case, a greater concentration of sugar.

On warming a sugary potatoe to 20^0C the sugar rapidly disappears, an increased portion of it is respired, and the rest reconverted to starch by another shifting of the equilibrium point, now in the opposite direction. We must not follow Muller's attempt to consider these factors quantitatively, but it is of interest that the balance of starch and sugar in these living cells of tubers, tree-trunks or winter-green leaves alters with temperature according to an established thermo-dynamical law. We cannot yet say to what extent physiological processes or biological adaptations are superposed upon this fundamental principle to produce so great an accumulation as to act as a satisfactory protection against winter frost.

<div style="text-align:right">F. F. BLACKMAN.</div>

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THE BRITISH ASSOCIATION AT WINNIPEG.

MANY members of the British Association were at first inclined to doubt the wisdom of arranging for another Colonial visit so soon after the South African meeting of 1905. However, as things turned out, the meeting at Winnipeg was a complete success, and was thoroughly enjoyed by most, if not all, who ventured to make the journey.   So far as Section K was concerned the attendance at the Winnipeg Meeting was nearly up to the average.   Unfortunately, only some nine or ten British botanists were able to attend, and only one from the Dominion (Professor Buller).   But this year we had the pleasure of meeting a consider- able number of American botanists, who in every way contributed greatly to the success of the meeting.   In addition to two fre- quent members of the Association, Professors D. H. Campbell and Blakeslee, the following, amongst others, were present :—Professor Cowles, of Chicago ; Professor Macbride, of Iowa ; Professor Overton, of Wisconsin ; Professor Livingston, of Baltimore ; Pro- fessor Ramaley, of Colorado ; Professor Praeger, of Kalamazoo and Professor Pollock, of Michigan.

The opportunity of personal intercourse with so many of one's fellow workers, which after all, forms one of the chief *raisons d'être* of the British Association, was enjoyed by everyone ; so much so, in fact, that Professor H. C. Cowles proposed at the usual Sectional Dinner, that a meeting of English-speaking botanists should be held in the near future, in Jamaica. The idea met with a good deal of approval.   Among the grounds given for the selection of this particular meeting place, were the following :—Jamaica is a British possession ; it is easily accessible to the Americans ; it would afford botanists a good opportunity of observing tropical vegetation under favourable conditions.

The local Secretary this year was Professor Buller, who kindly placed the convenient rooms of the botanical department of the University of Manitoba at the disposal of the section. The thanks of the members are due to him, and also to Professor Cowles, who, as Secretary of the Botanical Section of the American Association, took a great deal of trouble before the meeting, in arranging for the reading of papers by members from the United States.

In view of the close touch which Kew maintains with the Colonies, the selection of Colonel Prain as President of Section K for the Winnipeg Meeting, was singularly appropriate. A number of years have elapsed since the Section had a President whose interests are mainly centred in systematic botany. It was therefore fitting that Colonel Prain should select this branch of the science as the subject of his Presidential Address, which he delivered on Thursday morning, August 26th.

The Address dealt primarily with the aims and methods of work of the systematic botanist, and then went on to draw attention—not altogether unneeded in these days of extreme specialization—to the many points of contact between systematic botany on the one hand, and morphology, palæobotany, ecology, &c. on the other.

"The two-sided task of the systematist," said the President, "is to provide a census of the known forms of plant-life, and to explain the relationships of these forms to each other. The work on one side is mainly descriptive, on the other mainly taxonomic; but the two are interdependent, and their operations so intimately blended, that it is difficult to treat them apart." While "the descriptive student can hardly see the wood for its trees, the taxonomic student works in more open country, and can look upon the wood as a whole."

Colonel Prain defended the conservatism of method which is apparent especially in the descriptive worker, who still relies mainly on organography. On the other hand, the taxonomist finds imagination and originality as useful as the worker in any other branch of botany. The aims of the descriptive worker are primarily utilitarian; his results are means to the ends that others have in view. Those of the taxonomist, however, based as they are on phylogenetic study, stand in a sense, on a somewhat higher plane.

The President dealt at some length with the effect of the personal equation in descriptive work, which results in its extreme forms, in either "hair-splitting" or "lumping." He concluded that

"the ideal arrangement in monographic study, is the collaboration of two workers, one highly endowed with the discriminating, the other with the aggregating faculty. But for the statement of their final results, both must adopt the judicial attitude."

In discussing the apparent contradictions of existing systems of classification, Colonel Prain dealt with the difficulties of attempting to present a picture of such a system even in two dimensions. These difficulties are increased if a serial method of presentation is adopted. In the latter case, the differing points of departure adopted in different systems, result in a confusion, more apparent than real. In fact, to quote from the address—"dissension may be admitted, confusion there is none." The President himself suggested an illuminating conception, in three dimensions, of a natural system of classification. He imagined a closed spherical space, the surface of which is studded with symbols marking the relative positions of existing plant types. Within the sphere is a complex system of lines, radiating from the centre. These lines are constantly branching, at any point, at any angle, and in any plane. Some only of the lines reach the surface. In the abrupt terminals of other lines, we can dimly trace the vestiges of other spheres, once studded with symbols marking the existence of types now extinct.

But for an adequate presentation of this conception, as well as of other matters dealt with, the reader must be referred to the published Address itself (*Nature*, September 30th).

The remainder of Thursday morning was occupied by papers on a variety of subjects. To meet the convenience of members who wished to hear other addresses, the President postponed his until noon. Mr. J. Parkin opened the proceedings with a paper on the "Evolution of the Inflorescence." The paper was necessarily largely theoretical, and it would have been interesting to hear the evidence for some of the views put forward. This, however, will doubtless be forthcoming when the full paper is published. Mr. Parkin's view is that flowers were originally borne on the plant singly, each terminal to a leafy shoot. From such a shoot all inflorescences, as well as the solitary axillary flower, are to be derived. The single flower was succeeded by a simple dichasial cyme, such as is found in *Pæonia albiflora*. Racemose inflorescences are regarded as having always proceeded from cymose ones. Suggested steps in the evolution of the former are, an increase in the number of lateral flowers; suppression of tertiary branching,

and finally, arrest of the original terminal flower itself. The author also drew attention to what he terms " intercalary inflorescences," in which the main axis, after forming lateral flowers, continues its apical growth vegetatively. Examples are *Calluna, Callistemon,* &c.

Professor Douglas H. Campbell (Leland Stanford University) then gave a note on the Prothallium and Embryo of *Danæa.* No root is found till the embryo is of considerable size, and it then arises endogenously, in the centre of the embryo, probably from the stem-quadrant. The foot covers the growing point of this root, like a root-cap.

Professor D. T. Gwynne-Vaughan read a paper by Dr. Kidston and himself, on the " Ancestry of the Osmundaceæ." The authors hold that the Osmundaceæ and Zygopterideæ have arisen from a common ancestor. So far as the vascular systems of their stems are concerned, the two orders exhibit parallel lines of evolution. In both cases the primitive forms were protostelic. The central pith found in the more advanced types of both series, would seem to have arisen by the transformation of a central mass of tracheal elements into thin-walled parenchyma.

Further evidence for these views was afforded by a preliminary note contributed by Mr. W. T. Gordon, on the stem of *Zygopteris Pettycurensis,* a protostelic form which occupies the same position in the Zygopterid alliance as *Thamnopteris Schlechtendahlii* does in the Osmundaceous. It is interesting to note that though these two orders show almost exactly the same sequence of development, the Zygopterid series is much the older of the two. It began in the Calciferous Sandstone series, and apparently ended in the Permo-Carboniferous, while the Osmundaceæ originated in the Upper Permian and have continued down to existing times.

Professor A. H. R. Buller and Mr. C. W. Lowe gave an account of some observations on the number of Bacteria in the air of Winnipeg. They found that the number of micro-organisms falling upon a square foot of surface during one minute, varied from 3 in winter to 8,500 on a very windy day in summer.

In the afternoon Miss E. J. Welsford discussed some problems connected with the life-history of *Trichodiscus elegans,* an alga belonging to the Chætophoraceæ.

The rest of the afternoon sitting was occupied by an account by Mr. Parkin of the new industry of rubber cultivation. This paper aroused a good deal of interest amongst the audience, and was fully illustrated with specimens, lantern slides, instruments, &c.

On Friday morning Dr. Armstrong communicated a paper by Professor Willstätter, on the "Chemistry of Chlorophyll." Professor Willstätter's work is of course well known, but it was interesting to have a *resumé* presented to Section K. The paper laid stress on the differences, rather than the resemblances, between the respective pigments of blood and green leaves. While the molecule of hæmoglobin contains iron as its essential metal, in that of chlorophyll the iron is replaced by magnesium.

In contrast to the Dublin meeting, where physiology was so strongly represented, this was the only definitely physiological paper communicated. On the other hand, several of the ecological papers, which formed the chief feature of Friday morning's sitting, dealt with the physiological aspect of ecology.

Professor H. C. Cowles (of Chicago) led the way with a most interesting paper on "The Fundamental Causes of Succession among Plant-Associations." The author pointed out that ecological plant-geography is emerging, just as taxonomy and morphology have emerged, from the merely descriptive stage, and that the genetic relationships among plant-associations are now claiming attention. Recent work on the life-histories of these associations show that in general "edaphic formations" tend to develop into the "climatic formations" of the particular region. For this reason the author suggests the disuse of the terms edaphic and climatic, and their replacement by such terms as proximate and ultimate, which explicitly imply evolution. Intermediate stages between the proximate and ultimate or final, may be designated approximate, mediate and penultimate. In exceptional cases, where the external conditions may remain uniform for long periods of time, *e.g.*, in deserts, there is practically no succession, and the proximate and ultimate formations are the same. But in most cases, there is a sufficient, if gradual, change of conditions, and therefore succession is the rule. Even where the topography and the climate remain stable, the plants themselves gradually bring about such changes of conditions. Thus the accumulation of humus alters the water-content of the soil; increasing it, for instance, in a sandy upland soil, and decreasing it in low-lying, swampy soil. The increase of humus also materially affects the aeration, temperature and food-supply of the soil, and favours the growth of saprophytic fungi. A second important factor in succession is the influence of increasing or decreasing shade. Proximate upland associations are exposed to maximum illumination, while each succeeding stage is characterised

by an increase of shade. This favours those plants which need shade for germination, and opposes a check to those requiring light. Plant-invasions, the influence (chiefly destructive) of man, topographic and climatic changes, were also discussed as causes of succession. In general it is probable that every case of succession is occasioned by the co-operation of a number of causes.

Professor F. Ramaley (of Colorado), in a paper on the relations of the Flora of the Rocky Mountains to Climate, concluded that in the main it is temperature, rather than topography, soil or rainfall, which permits or restricts the extension of plants over wide areas.

Professor B. E. Livingston (who has recently been appointed to the new Chair of Plant Physiology at the Johns Hopkins University of Baltimore) next gave an account of the porous cup atmometer as an instrument of ecological research. Dr. Livingston laid great stress on the importance of the measurement of evaporation in the systematic study of plant environments. " A properly constructed atmometer " (or evaporimeter), said he, " will automatically sum the various meteorological elements as they influence the plant, and may be said approximately to integrate the march of plant environment above the soil surface. From the curve of evaporation for the growing season in any region, together with the rainfall and certain physical data in regard to the soil, the general nature of the vegetation, in an ecological sense, may be quite clearly deduced." The author then described the porous clay atmometer which he himself devised, and has extensively used. A number of useful precautions to be observed in its use were suggested.

Professor R. H. Yapp gave the results of some observations and experiments on *Spiræa Ulmaria*. The curious seasonal differences found in this species, in respect to the formation of glabrous and hairy leaves, had been previously described. It was now shown that these differences correspond in a remarkable way with the vertical differences (due to stratification of the vegetation) and also to the annual march, of evaporation and light intensity. Attention was also drawn to the marked similarities in the distribution of (1) anthocyan in young leaves, (2) hairs on partly hairy leaves of *Spiræa*, and (3) withering in leaves in exposed situations.

Professor Pammel (of Iowa) in discussing the delayed germination of seeds, showed that exposure to the rigorous conditions of winter resulted in more rapid and perfect germination than housing in a dry condition until the spring-time.

In the afternoon Mr. Harold Wager gave the semi-popular lecture on "The Perception of Light in Plants." Mr. Wager's views on this subject are well known, as they have been recently published. It will therefore suffice to say that he suggests, as an alternative to Haberlandt's theory, that the chlorophyll grains of foliage leaves are the organs which perceive the direction of the incident rays of light. The lecture attracted a large audience, and was illustrated by a number of exceedingly beautiful lantern slides.

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Monday, August 30th, was devoted to a joint discussion on "Wheat," by the chemical, botanical and agricultural sections. The first paper read formed the only botanical contribution to the discussion. This was by Dr. Otto Stapf, on "The History of the Wheats." There are some ten principal races of wheat known to agriculturists. These are usually grouped into the "wheats proper" and the "spelt wheats." The former possess tough spindles, grains loose in the husk, and thick pericarps: the latter, brittle spindles, grains tightly enclosed, and thin pericarps. These are important practical differences, and at first sight are apparently also of considerable taxonomic importance. But Dr. Stapf shows that in each case the three characters behave functionally as one, and can therefore be disregarded in attacking the problem of phylogeny. In fact, the author concludes that the practical division into "spelts" and "proper" wheats, does not in any way represent true affinities. He is of opinion that all the modern varieties of wheat may be traced back to some four (or possibly only three) primitive wild forms. All these had their home in a comparatively restricted area, which included South-eastern Europe, Asia Minor, Syria, &c.

Papers were also read by a number of English and Canadian chemists and agriculturists. Amongst the subjects discussed were the following:— the factors determining the yield of wheat: the influence of environment on the composition of the grain: the strength of wheat: wheat breeding, &c.

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The interest was well sustained to the last, and on Tuesday morning, August 31st, a number of papers were read, dealing chiefly with mycological and cytological questions.

The first paper was by Professor A. H. R. Buller (of Winnipeg), on the "Spores of the Hymenomycetes." The author described a number of interesting features connected with spore dispersal. Amongst the points touched upon were the number of spores
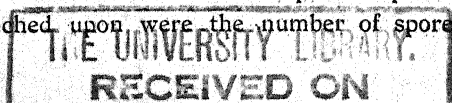
formed : the rate of fall : the path of the falling spores, &c. The paper was fully illustrated by models, diagrams, slides, &c. It was mainly a *resumé* of some of the more important results contained in Dr. Buller's recent book " Researches on Fungi."

Professor J. B. Overton (of Wisconsin) gave an account of his work on the nuclei of *Podophyllum peltatum.* Professor Overton carefully traced the changes in the telophase chromosomes during their passage into the resting nucleus. He found that they undergo progressive internal vacuolization, and so become much enlarged. Each chromosome finally consists of a reticulum of linin, supporting the chromatic granules. The author, who is strongly convinced of the " individuality of the chromosomes," believes that the resting reticulum is composed of a number of these independent, elementary reticula.

Dr. H. C. I. Fraser read a paper on " The Nuclear Phenomena of Ascomycetes, and their Relations to Heredity." Various types of fertilisation, both normal and degenerate, were described. In all cases fertilisation is followed by a second (asexual) fusion of nuclei in the ascus. Both fusions are followed by reduction divisions, but these differ in character in the two cases.

Mr. Harold Wager, in collaboration with Miss Peniston, gave an account of the nucleus of the Yeast plant. The position taken up by the authors is substantially the same as that of an earlier paper by Mr. Wager (1898). In brief, this is that the nuclear apparatus of the yeast cell consists of a nucleolus, in contact with a vacuole, the latter being surrounded by a chromatin network. A number of further points, however, were elaborated in this paper. For instance, the amount of chromatin present appears to vary with the state of metabolic activity of the cell. There is some reason to think that the nuclear vacuole may play an important part in the elaboration of chromatin.

Papers were also contributed by Dr. R. R. Gates, on the effect of tropical conditions on the growth of some English Oenotheras, and by Professor H. L. Bolley on the control of weeds by means of chemical sprays.

Excursions.

During the meeting several botanical excursions were arranged by Professor Buller. The first of these was to the shores of Lake Winnipeg, where some fine poplar forests and marshes were examined. Other excursions were to Elm Park on the Red River

(deciduous forest and river bank vegetation), and to Hedingly, the latter being situated on uncultivated prairie.

But naturally the most enjoyable excursion was that to the Pacific Coast. The time (some nine or ten days) occupied by this was far too short, but in spite of this, the botanists were able to gather some valuable impressions of the general character of the diverse vegetation passed during the journey. After all, there is perhaps an element of truth in the dictum of Stevenson, that "A country rapidly passed through under favourable auspices may leave upon us a unity of impression that would only be disturbed if we stayed longer." [1]

For several days after leaving Winnipeg, we journeyed westwards over the vast prairie. Though numerous Asters, Solidagos, &c., were in flower, the prevalent colours were different shades of brown, broken at frequent intervals by the green of bushland, or the deep crimson of "alkali" patches. The latter are abundant in shallow depressions on the prairie, and contain such plants as *Salicornia herbacea, Suæda linearis, Atriplex,* &c.

The Rocky and the Selkirk Mountain ranges, with their magnificent conifer forests, formed a pleasing contrast to the less ambitious scenery of the plains. Some of the more abundant Conifers forming these forests were *Picea Engelmanni, Pseudotsuga Douglasii, Tsuga Mertensiana, Pinus monticola,* and further to the westward, *Thuja plicata.*

The special train made considerable stops at Banff, Laggan and Glacier, so that in addition to enjoying the grandeur of the scenery, we had an opportunity of examining the characteristic vegetation at somewhat closer quarters.

Here and there, right along the track of the Canadian Pacific Railway, great tracts of forest exhibited nothing but bare and blackened trunks, which bore witness to the frequency and extent of disastrous forest fires. Vegetation soon springs up after these fires, but it is long before the Conifers recover their earlier supremacy. The first stages of tree-succession in this region, appear to consist chiefly of *Populus tremuloides* and *Salix rostrata.*

On reaching Vancouver, the party at once proceeded by boat to Victoria. Here the land vegetation had a more English appearance than any we had hitherto seen. Several of the botanists spent an enjoyable morning in a boat, examining magnificent groves

[1] R. L. Stevenson, in "An Autumn Effect."

of *Nereocystis*, some specimens of which, when measured, proved to be upwards of fifty feet in length.

On the return journey some time was spent in Stanley Park, at Vancouver. This consists of an extensive area of luxuriant temperate rain-forest; many of the trees, especially the Cedars (*Thuja plicata*) and Douglas Firs (*Pseudotsuga Douglasii*) being of enormous size. A striking proof of the durability of the wood of the former was afforded by the manner of growth of some of the trees. In the humid air of this forest it is of common occurrence for seedlings to establish themselves on the top of fallen trunks. In some cases the seedlings had grown into huge forest trees, which had themselves ultimately perished, while the wood of the tree on which they had perched as seedlings still defied decay.

On returning to Calgary, we turned north to Edmonton, and thence proceeded, by the Canadian Northern Railway, to Winnipeg.

From the point of view of the botanists, the pleasures of the western trip were much enhanced by the presence of Professor H. C. Cowles, and, on the return journey, of Professor Macoun, the Dominion Government Botanist, as well; both of whom were thoroughly acquainted with the flora of the region.

In addition to the official excursions, several members visited other parts of interest. For instance, the present writer spent some time before the meeting amongst the woods and swamps of Northern Minnesota; while other members visited the Valley of the Nipigon, the Lake of the Woods, or made botanical excursions from Toronto or Chicago.

<div align="right">R.H.Y.</div>

GERMAN VEGETATION.

DIE PFLANZENWELT DEUTSCHLANDS, Lehrbuch der Formationsbiologie, eine Darstellung der Lebensgeschichte der wildwachsenden Pflanzenvereine und der Kulturflächen, von DR. PAUL GRAEBNER. Leipsig, 1909, Verlag von Quelle & Meyer, Pp. XI. and 374. Price 7 marks.

THIS very readable account of the natural plant-communities of Germany, by Dr. Graebner, already well-known as the author of " Die Heide Norddeutschlands "—one of the most thorough of existing ecological studies of a single great plant-formation—and as the collaborator with Professor Ascherson in the standard " Mitteleuropäischer Flora," will be of particular interest to British students of vegetation, since it furnishes one of the first opportunities of systematically comparing the plant-communities of a neighbouring country with those of our own.

In laying down his principles for the classification of plant-communities, Dr. Graebner sets out from those which are developed under the most favourable conditions of climate and soil, namely the rain-forests of the tropics, which produce the greatest annual " crop " of vegetable material in the world. Among these conditions —besides the well-known factors of continuous warmth, abundant and distributed rain-fall, etc.—he lays stress on the poverty or absence of humus (owing to the rapid oxidation of the fallen leaves and branches) and the consequent free aeration of the soil. Starting with the ideal growth-conditions of the tropical rain-forest he traces the gradual incoming and increasing dominance of factors adverse to vegetation as we pass on the one hand into regions with well-marked dry periods and thence into the sub-tropical deserts, and on the other into the colder temperate and arctic regions, where drought and winter, respectively, impose upon plants a longer and longer resting period. This progressive diminution of vegetative activity is accompanied, of course, by a progressive decrease of the annual " crop " of material produced. The responses of plant-form and life-history to these great climatic factors are briefly but skilfully expounded, and the author then proceeds to consider the other class of ecological factors—those connected with soil. Here also the appearance of adverse conditions is accompanied by a decrease in the mass of material annually produced. On " good " soil a large crop is produced, on " poor " soil a small one. But the " goodness " of a soil does not depend only on the amount of available mineral food, it is also greatly influenced by various other physical and chemical factors :—texture, air- and water-content, presence of humus and the like. Where humus, especially " Rohhumus " (dry peat), is formed on the surface, aeration of the soil is so much hindered that the plants are all shallow-rooting, and the same effect is produced by the presence of a hard layer fairly close to the surface, which physically prevents the roots penetrating to deeper layers. This hardening of the surface or limitation of the depth of the soil has a most important effect on the plant-covering, excluding many species altogether, and, in general, leading to a dwarfing of the vegetation; so that, as the author remarks, " the same soil under the same conditions of moisture and warmth may bear perhaps in one place the finest high forest, in another only

heath vegetation." Besides, these factors there are, of course, the special chemical factors, such as the presence of common salt, which profoundly alters the vegetation, since only specially adapted plants which can tolerate it are able to exist at all.

Dr. Graebner points out that since the existence of any plant-community in a given spot is due to the combined effect of a number of factors developed in different degrees, it is not easy to decide which to choose as a basis for primary classification. In the case of a country like Germany, however, where variations of climate are certainly not of the first importance, the problem is practically limited to choosing between the edaphic or soil factors. This, of course, is also the case in the British Isles. At first sight it would appear that the water of the soil—that fundamentally important factor in the life of a higher plant—is the natural factor on the variations of which we should base our primary classification, and this is the usual method adopted, for instance, by Warming in his earlier work. But Dr. Graebner is of opinion that this involves so many contradictions that such a principle does not, in fact, yield a natural classification. Thus the soil of an open heath and of a deciduous wood may possess the same water-content, and so may a Fen (Wiesenmoor) and a Sphagnum-moor (Hochmoor), and yet they are fundamentally different plant-communities, possessing different floras. The heath, the Sphagnum-moor and certain types of wood on the one hand have a whole series of characteristic species in common and so on the other have the open hills, rocks and other types of wood. It is true that Warming and others try to get over this difficulty by distinguishing between "physical" and "physiological" soil-water, *i.e.*, between the total water-content of the soil and that which is actually available for the roots of the plants, but although this distinction is of great importance, by no means all the anomalies of the classification by water-content are removed by its aid, nor do we know the facts accurately enough to employ it with precision. Dr. Graebner proposes to classify plant-communities on the basis of the total crop of vegetable material produced in the year, using this as an index of the "fertility" or "poverty" of the soil, itself due, as already shown, to very various factors. On the "good" soils the most luxuriant vegetation will flourish, excluding the slower growing, while on the "poor" soils the former will no longer be able to exist and will give place to a less exacting type of plant-community.

The author thus divides the plant-communities of Germany into three great series: (i) those in which the physical and chemical conditions are favourable (apart from water-content); (ii) those in which the plants are only able to obtain a small amount of food from the soil, even in favourable seasons; (iii) those on salty ground, where the conditions of life are of course quite special. These three series are then again divided according to the water-content of the soil.

Roughly speaking the first series may be said to contain steppe (dry), natural meadow- and forest-vegetation (damp), as well as fen and most aquatic vegetation (wet), while the second is equivalent to the great heath-series, with the "sandy plain" (dry), the true "heath" (damp) and the "Hochmoor" (wet).

As Dr. Graebner remarks, this method has at any rate the advantage of separating, in the first instance, series of formations which are very clearly distinct, both in type of vegetation

and in constituent species, and the primary principle of division is probably the soundest within an area of fairly uniform climate.

Dr. Graebner's complete scheme, really based largely on the principle of "limiting factors," is one of the most helpful we have met with, though it can undoubtedly be criticised adversely in various details.

In the "special part" of Dr. Graebner's book, we have very readable and interesting accounts of the different German plant-communities. Most of these are essentially like our own, though with a considerably richer flora.

The vegetation of "sunny hills" described by Graebner (often called "Pontic" vegetation) has much in common, both in general ecological conditions and in actual species, with that of our chalk downs. Some of Watson's "Germanic" species, found only or mainly in the south-east of England, are characteristic of these "sunny hills." "Sandy plains" with a characteristic vegetation are not common in this country, but possibly a parallel may be found in parts of our East Anglian heaths.

Ruderal plants, weeds of arable land and of gardens, show as might be expected great similarities and often identity with our own.

Of Alpine meadows we have none strictly comparable with those of Central Europe, and our grassland above the limit of trees on the higher Scotch mountains has scarcely been sufficiently studied to enable a useful comparison to be made. Of woods, Dr. Graebner distinguishes among "Laubwälder" (i) Beech, (ii) Oak, (iii) Mixed, and (iv) Birch. The German beech-woods are much more widely distributed than our own, and have apparently greatly decreased in extent, for the reason that they naturally occupy the best soils, which have been largely cleared for agriculture. The German beech-woods which occupy, according to Graebner, mostly marly soils, correspond, no doubt, to those which in England are practically confined to the chalk of the south-east. We are probably justified in concluding that the English beech-woods also at one time covered large tracts of our East Anglian chalk which is at present one of the best of our wheat growing areas, and on which but few remnants of woodland remain. Over the rest of England the Ash is dominant on limy soils, alone on the purer, and mixed with the Oak on those with a lower lime-content. Graebner does not mention ash-woods of this type as existing in Germany. We may therefore conclude that the south-eastern English beech-woods on chalk represent the extreme north-western of the continental woods, and that beyond the limits of these they are replaced by ash-woods. In southern England we have another type of beech-wood, locally developed on sands. This type is not mentioned by Graebner, though it has a fundamentally different type of ground flora. It is not, however, unknown on the continent, since it is described by Warming. The general type of ground flora characteristic of Beech-woods on limy soil is naturally much the same in Germany as in England, since the characteristics of the dominant tree are so strongly marked. Many species of course occur in the German woods which are absent from the English ones, but the flora is still described as "poor," and is scarcely likely to be so rich as that of our Ash and Ash-Oak types, the richest of our native woodland types.

Oak-wood is another widely distributed German type, though it scarcely seems to occupy so predominant a position as in this

country, since the Oak appears to be excluded by the Beech on many German soils. One does not gather from Graebner's account that there is any distinction in Germany between woods of *Quercus sessiliflora* and those of of *Q. pedunculata*—a distinction so well-marked in England. On the other hand oak-woods on wet soil in which actual peat-formation occurs (Auenwälder of Drude) are scarcely well represented in this country, though our oak-woods show a transition to alder-woods in such situations. The general ecological characteristics of the oak-wood are much the same in Germany and England, though again they have many species which we have not. The Ivy and the Honeysuckle are the characteristic climbers in both cases.

The "mixed woods" of Germany are not represented in this country. In richness of arboreal and ground flora they seem to stand nearest to our Ash-Oak-woods, but are said to be developed on "fresh" glacial and other sands, rather than on limy soil. The richness of the flora is attributed to the different depths at which the various trees root, allowing a greater variety of shrubs and herbs to find space for their root-systems.

Of the Birches, *B. verrucosa* is said to be the most generally distributed, while *B. tomentosa* occurs in the more rainy north-west, where in the great heath-region it is mixed with the other species. This is interesting in view of the fact that a similar mixture of the two birches occurs on the heaths of the south-east of England, probably to be regarded as an extension of the German heaths, while *B. tomentosa* is the characteristic form of the hill woods of the north and west of our country.

Dr. Graebner regards birch-woods as mostly a transition to heath, to sandy plains and to the sunny hill communities, and points out that this type of woodland does not possess a characteristic ground-flora as such, the trees being intermingled with plants belonging to the allied non-arboreal vegetation, such for instance, as the heath flora. This description fits very well the birch-woods of this country. With us too the non-exacting character of the birch leads to a development of loose woods on the borders of heaths, etc., while birch-wood also forms a climatic zone above the oak-woods, and sometimes above the ash-woods also, of our higher hills.

Of the well-developed coniferous forests of Germany we have no representatives in this country, with the exception of the Scottish pinewoods.

The remainder of the plant-communities described by Dr. Graebner—Alder-woods, Fens, River-bank vegetation, Aquatic vegetation, Heath, "Hochmoor," Coastal dunes and Salt marshes—are more or less closely paralleled in England. It should be noted, however, that what he calls "Heidemoor" which is generally dominated by *Sphagnum*, is not the same thing as our "Heather-moor" (used for grouse-shooting) which is a drier type, more closely approaching Heath. Our extensive moors of *Eriophorum* and of *Scirpus cæspitosus* do not appear to be represented in Germany, since all Dr. Graebner's references to these plants show that they occur merely as local societies or as more or less isolated individuals. A thorough ecological study of the extensive series of "Hochmoor" types of the British Isles is one of the things which British ecologists should take in hand as soon as possible.

An interesting feature of Dr. Graebner's book is the addition of a short account of the animal life of each plant-community, contributed by Oberlehrer F. G. Meyer. The work is illustrated by a number of text-figures of the habit of characteristic plants belonging to the different communities and by a few views of vegetation.

The book would we think have been improved by regular lists of species belonging to the various plant-communities with indications of dominance, relative abundance, etc.

The treatment of the effect of humus scarcely brings into sufficient prominence the important distinction between " Milde Humus " and " Rohhumus," and we miss also an adequate treatment of the problems of succession, without which it is impossible to obtain a just conception of the problems of vegetation and of the true relationships of the different communities. It is rather on this line, together with intensive study, that we must look for an increase in the definiteness of our concepts of vegetation units, without which we cannot hope to attain to a really natural classification of these units. A.G.T.

NOTES ON RECENT LITERATURE.

RECENT PROGRESS IN THE STUDY OF THE EMBRYO-SAC OF THE ANGIOSPERMS.

THE female gametophyte of the Angiosperms has long been regarded as "a morphological problem of great obscurity."[1] While the monophyletic origin of Angiosperms from a Gymnospermous stock is now assumed by most authors,[2] the gulf between the archegonium-bearing prothallus of a typical Gymnosperm and the eight-nucleate and bipolar embryo-sac of the Angiosperm has proved a very difficult one to bridge. Among the Gymnosperms, the embryo-sac of *Gnetum*, with its egg organised at the free-nuclear stage, seemed till recently to offer the nearest approach to Angiosperm conditions; but even here no clue was found to the phylogenetic origin of the endosperm in the latter group. The disputed morphology of this tissue has been the great difficulty in interpreting the embryo-sac of the Angiosperm in terms of that of the Gymnosperm. Normally, it is formed after fertilisation by the division of a fusion-nucleus consisting of the two polar nuclei and a male nucleus[3]— and until recently no tissue comparable to this in origin has been described in a Gymnosperm.

Before discussing the light thrown by recent work upon the phylogeny of the embryo-sac, it may be of interest to touch briefly on some of the principal suggestions that have been advanced to account for its homologies and possible origin. Strasburger in 1879 suggested[4] that the eight nuclei in the embryo-sac represent

[1] Coulter and Chamberlain (03), p. 88.
[2] See, however, Campbell, " Evolution of Plants," 1899, p. 155, and " Mosses and Ferns, 1905, p. 605; also Coulter and Chamberlain, 1904, pp. 283-287.
Sargant 1908, p. 126. [4] Strasburger 1879, pp. 137-139.

a prothallus whose development before fertilisation has stopped at that stage, the further development of the prothallus so formed being the result of a nuclear fusion which acts as a stimulus to renewed division. This view was generally held until the discovery that a male nucleus entered into the fusion, when it became necessary to explain the phylogenetic origin of the so-called "double fertilisation." Various suggestions[1] were made, of which the one most favoured was that of Sargant—that the union of the upper polar nucleus (sister of the egg) and the male nucleus may be a true fertilisation, but that the introduction of the lower polar nucleus causes the transformation of the embryo which should have arisen from this union into a monstrous short-lived tissue, serving for the nourishment of the embryo.

Strasburger's hypothesis regarded the antipodals as merely prothallial cells which have lost their original function and are now of an evanescent nature, except when they have taken on a new function, that of absorbing food from the nucellus. Many later writers, however, have considered that the polarity of the antipodal group, as compared with the egg-apparatus, and the behaviour of these cells when they do function, suggest that they represent the vegetative tissues of the gametophyte. This view has gained its chief support from Lotsy's investigations on the embryo-sac of *Gnetum gnemon*,[2] which he described as containing a sterile prothallus in the lower part, and free fertile nuclei in the upper.[3] The Angiosperm embryo-sac has been compared with this, the antipodals and lower polar nucleus being considered as equivalent to the sterile vegetative portion, and the egg apparatus and upper polar nucleus to the fertile nuclei.

Lotsy himself, however, deduced other homologies from *Gnetum gnemon*. He regarded the antipodal cells as equivalent to a degenerate egg-apparatus, and the two egg-apparatus thus present in the sac as representing the remains of the archegonia—the rest of the prothallial tissue being reduced to the two polar nuclei. Somewhat similar homologies have lately been elaborated by Porsch,[4] who considers that in the Angiosperm we have a prothallus so reduced as to consist solely of two archegonia, represented by the egg-apparatus and the antipodals respectively. He even homologises the cells composing these two groups with the components of an archegonium—thus the synergids represent the neck-cells, and the two polar nuclei are the ventral canal cells of the two archegonia; and as the ventral canal cell is the sister of the egg, he regards triple fusion as a kind of fertilisation and the endosperm as a modified embryo. In considering this theory, it must be remembered that the archegonium in Gymnosperms appears at a much later stage in the life-cycle, and that it is necessary to explain how such a specialised structure could be represented in so reduced a gametophyte as that of the Angiosperms. Moreover, the archegonium itself has disappeared in the highest group of the Gymnosperms, so that in *Welwitschia* and *Gnetum*

[1] Sargant, 1900; Land, 1907; Thomas, 1907; Berridge, 1907.
[2] Lotsy, 1899.
[3] Coulter, 1908 (B), however, describes the embryo-sac in this species as containing only free nuclei, Lotsy's sterile prothallus being, according to him, merely deeply staining "pavement tissue" of the nucellus at the base of the sac.
[4] Porsch, 1907, pp. 19, 20.

free nuclei function as eggs. This view would therefore entail giving up all connection between the Gnetales and the Angiosperms —a connection which recent work has shown to be probable.

In the above brief summary no account has been made of certain exceptions to the general rule that the Angiosperm embryo-sac is bipolar and contains, at the end of free nuclear division, no more than eight nuclei. These exceptions will be discussed later; it suffices at present to note that they have been used as instances in support of most of the theories mentioned above. It is both interesting and instructive to note how they have been used by various investigators to uphold the most fundamentally different hypotheses; and the existence of such widely divergent explanations of the same set of facts shows how much some new data were needed to confirm or correct these theories. Such data have recently been furnished by Pearson's researches on *Welwitschia*,[1] in which he has found a process of endosperm formation which can be closely paralleled with that seen in the Angiosperms. In the embryo-sac of *Welwitschia*, all the nuclei at the end of free nuclear division are potential gametes. Some of them remain free, and can function as gametes, but the majority fuse in groups of six to twenty to form a number of primary endosperm nuclei, by whose division the cellular endosperm is produced. Such a method of endosperm formation is unknown in any of the lower Gymnosperms, but there are indications that more detailed investigation will show that similar processes take place in *Gnetum*.

An endosperm which originates from fusion nuclei at once suggests a comparison with that of the Angiosperms, and Pearson has suggested that the endosperm of the primitive Angiosperm was homologous with that of *Welwitschia*—that "in a broad sense, the Angiosperms and Gnetoideæ" (*Gnetum* and *Welwitschia*) "are derived from the same stock," the Gnetoideæ being probably "the last representatives of a race which separated from the main Angiosperm line."[2] This implies that the embryo-sac of the primitive Angiosperm contained many free nuclei, all potential gametes, and a large number of primary endosperm nuclei, formed by the fusion of these gametes. In *Welwitschia*, free nuclear division stops at the eleventh generation from the megaspore, and in a similarly constituted sac, as a result of the progressive reduction that has always marked the gametophyte, it is easy enough to imagine free nuclear division stopping at successively earlier stages, until it now ends as a rule at the third generation from the megaspore. With this reduction in the number of nuclei, the number of those available for fusion would decrease, until now there are only sufficient to form one primary endosperm nucleus.

If this hypothesis is correct, the eight nuclei which now, in normal cases, represent this reduced gametophyte, are all to be regarded as potential or reduced gametes. In the great majority of cases, the egg is the only one now functional; nevertheless there are instances in which others of the eight nuclei have shown that they may possess similar potentialities. Thus several cases have been described in which the synergids have been fertilised and produced embryos[3], and fertilisation of an antipodal has been seen

[1] Pearson, 1909.   [2] Pearson, 1909, p. 386.
[3] Dodel, 1891, *ex* Coulter and Chamberlain, 1903 p. 217; Overton, 1891, *ex* Mann, 1892, p. 373; Guignard, 1901.

in a species of *Aster*.[1] In *Juglans*,[2] no egg-apparatus is organised, the three micropylar nuclei remain free, and any one of them may be fertilised. These instances are of course exceptional, but they are indications that there is probably no serious difficulty in the way of regarding all the nuclei in the sac, other than the egg, as representing gametes which were once free and potentially sexual. These have now become specialised, until, with the exception of the polar nuclei, they are no longer free nuclei, but cells, and are either functionless and evanescent (the antipodals in most cases) or have acquired new functions (the synergids usually, and the antipodals where they assist in the nourishment of the sac). The polarity of the Angiosperm sac and the occurrence of double fertilisation (triple fusion) are the chief difficulties in the way of adopting this scheme. As regards the former, the difficulty is perhaps less than it appears at first sight. In *Welwitschia* the sac at the two-nucleate stage is bipolar, as in the Angiosperm, but as nuclear division proceeds with great rapidity, while the increase in size of the sac is slow and no central vacuole is formed, this polarity is lost, the nuclei becoming evenly distributed. As the nuclei became fewer, with the organisation of the egg in successively earlier generations, the probable slowing-down of division in relation to the enlargement of the sac would result in the formation of a central vacuole at a relatively early stage, and a consequent grouping of the first-formed nuclei. Triple fusion also may be explained as a consequence of this decrease in the number of nuclei formed; no process that can be regarded as comparable with it occurs in *Welwitschia*, where the unused male nucleus merely degenerates, and it is probable that the same was the case in the primitive Angiosperm. Pearson suggests that triple fusion was adopted when the decrease in the number of nuclei available for fusion, with the consequent reduction in the number of primary endosperm nuclei, and therefore of the amount of endosperm formed, had decreased the efficiency of the endosperm as a feeding tissue. The amount of such tissue formed by each fusion-nucleus in *Welwitschia* is small, and in a sac containing only one of these nuclei the developing embryo would have but a poor food-supply, unless the efficiency of this endosperm could be increased. The introduction of a male nucleus into the fusion would, as in the case of the fertilised egg, increase the stimulus to growth, and " direct advantage would seem to accrue to the embryo from the supply of a food substance of the same double origin as itself." [3] The steps by which triple fusion was initiated must remain con- jectural, but it may be pointed out that the construction of the Angiosperm sac, with its central strand of protoplasm along which the polar nuclei move, is very favourable to the possibility of the unused second male nucleus being drawn into their fusion. It should also be noted that though endosperm formation consequent on a triple fusion has thus probably become the rule among Angiosperms, cases are occasionally reported[4] where the primary endosperm nucleus has, as in *Welwitschia*, given rise to a certain amount of endosperm *before* fertilisation.

[1] Opperman, 1904.
[2] Nawaschin and Karsten, *ex* Coulter and Chamberlain, 1903, pp. 90, 91.
[3] Thomas, 1907, p. 426.
[4] Coulter, 1898, p. 83; Du Sablon, 1908; Stephens, 1909, p. 368; Cook, 1909, p. 57.

The above is a mere outline of Pearson's main argument; further evidence must be sought in his paper. It has been too recently published for adequate comment to have been made on it, but whatever criticisms may be in store, the facts he describes will always be of far-reaching importance in any discussion of the morphology of the embryo-sac, and in his argument we find both an important clue to the origin of the endosperm and the most probable phylogeny yet suggested for the embryo-sac of the Angiosperms.

In the above brief sketch of current ideas on the morphology of the embryo-sac, we have purposely avoided much debatable ground and many disputed facts by writing as if the authors of these theories had only to take into account the normal eight-nucleate and bipolar sac. Now we must consider what bearing certain exceptions to this normal rule have on these questions. In the first place, there have been described several sacs which are not bipolar, and in which free nuclear division stops at the fourth instead of at the third generation, so that they contain sixteen nuclei instead of eight. At first sight these would seem to be instances of the preservation of a relatively primitive type of embryo-sac, and as such, these cases have been used to uphold most of the theories noticed above. But on the other hand, there has been some discussion as to whether these forms are not to be regarded as specialised from the normal type rather than primitive, and since this question is still unsettled, we have reserved them for discussion at this point.

The following are the cases referred to :—

1. In *Peperomia*[1] the first two divisions in the embryo-sac give rise to four nuclei, arranged "like the spores of a tetrad," whose further divisions result in sixteen nuclei, scattered through the sac. One of these functions as an egg-nucleus; of the remainder, eight (usually) in *P. pellucida*, *P. arifolia* and *P. sitensii* and fourteen in *P. hispidula*, fuse to form the primary endosperm-nucleus and the remainder ultimately degenerate.

2. In three genera of the order Penæaceæ[2] (the remaining genera have not been investigated), the first two divisions form a tetrad of nuclei arranged just as in *Peperomia*; these separate, and each again divides twice, so that four groups of four nuclei each are formed at the periphery of the sac. Cells are organized round three of the nuclei in each group, in the form of an egg-apparatus, and the four remaining nuclei move to the centre and fuse to form the primary endosperm-nucleus. *Euphorbia procera*, at the earliest stage known, shows four nuclei at the periphery of the sac, whose further behaviour is exactly that of the first four nuclei formed in the Penæaceæ; but the earlier history of these nuclei has not been followed out.

3. In *Gunnera* the first four nuclei are again tetrahedrally arranged. They undergo four successive divisions, and of the resulting sixteen nuclei, three form a micropylar egg-apparatus, six form an antipodal cell-group, often in two sets of three cells, and the remainder fuse to form the primary endosperm nucleus.

On the hypothesis that these types of sac are primitive, they

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[1] Campbell, 1899, 1901 ; Johnson. 1900, 1907 ; Brown, 1908.
[2] Stephens, 1909.

may be regarded as forms in which the gametophyte, while retaining a relatively primitive number of nuclei, has evolved along three divergent lines.   On the other hand, those who regard them as specialised from the ordinary form explain the presence of the sixteen nuclei in the following way : It must be remembered that in most cases the embryo-sac is the one surviving and developing member of a row of four spores, so that five successive divisions (two to form the spores and three the eight-nucleate embryo-sac within one of these spores) intervene between megaspore mother-cell and egg.   Undoubtedly this is more primitive than the state of affairs found in such a form as *Lilium*, where no row of spores is formed, so that only three divisions intervene between mother-cell and egg.   Now, in *Peperomia, Gunnera*, and the Penæaceæ the early stages have been carefully studied to determine this point, and in each it is found that the mother-cell forms no row of spores, such as would be expected in a relatively primitive form, so that only the four divisions which form the sixteen nuclei intervene between megaspore mother-cell and completed embryo-sac.   This fact, in conjunction with the tetrahedral arrangement of the nuclei formed by the first two divisions (an arrangement so common among spores) has been thought by some botanists[1] to indicate that in these cases the embryo-sac includes four megaspore nuclei, each of which divides twice.   It is significant in this connection to note that genera allied to *Peperomia* (*Piper*[2] and *Heckeria*[2]) and to *Gunnera* (*Hippuris*[3]) form a row of four spores, from one of which a normal embryo-sac is produced.

This conception of the production of one embryo-sac from four megaspores, which germinate simultaneously, has even been extended to all cases in which—to use the current phrase—the mother-cell becomes the embryo-sac directly, the formation of spores being omitted.[4] Coulter is the chief exponent of this view ; he holds that the nuclei formed by the reduction division in the mother-cell are always to be regarded as the nuclei of four spores, whatever may be their subsequent history—so that in a case like *Lilium*, where there are only three divisions from mother-cell to egg, the gametophyte consists of only one generation of free nuclei.

This view has naturally excited a good deal of controversy ; the arguments that have been advanced for and against it may be summarised under four heads :—

1.   Five, four or three successive nuclear divisions intervene between mother-cell and egg in the Angiosperms.   The first two divisions in the mother-cell (heterotype and homotype) show the same characters throughout the plant-kingdom, and always result in the formation of four spore-nuclei containing the gametophytic number of chromosomes.   The further divisions of each of these nuclei are of the ordinary type, and belong to the gametophytic generation, whether this is formed from one spore only, or is a compound structure formed by the simultaneous germination of several spores within the mother-cell.

Against this view it is argued that there is a general tendency in vascular plants to reduce their sporogenous tissue.   " Since we can trace the reduction of these divisions until among angiosperms

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[1] Coulter, 1908 ; Brown, 1908, etc.   [2] Johnson, 1902.   [3] Fischer, 1880.
[4] Lloyd, 1902, Davis, 1905, p. 471 472 ; Pace, 1908, 1909 ; Coulter, 1908.

the archesporial cell may without dividing form one megaspore mother-cell, it does not seem reasonable to suppose that the division of the mother-cell to four megaspores may not also be left out, and the mother-cell function directly as a megaspore.[1] " The reduction-division would then be shifted so as to take place at the germination of this spore.[2]

2. On Pearson's hypothesis, at the end of free nuclear divisions all the nuclei in the embryo-sac—whether one, two, or four spores germinate within it—are potential or reduced gametes. If this view is accepted, it will be evident that the embryo-sac is much more plastic in its ontogeny than was formerly supposed. The usual grouping of the nuclei at the two ends of the sac (seen in the eight-nucleate sac and also in *Gunnera*) is a natural consequence of the elongated shape it assumes and the formation of a central vacuole. A striking parallel is seen in *Hyacinthus orientalis*,[3] where the microspores sometimes germinate like megaspores, with three successive mitoses, giving rise to four nuclei at each end of the pollen-grain, with a large central vacuole. Moreover, in various apogamous species, where the reduction-division does not occur, and the normal row of four megaspores may be suppressed, development of the embryo-sac follows the usual course. The fact that there is no grouping in *Peperomia*, and that in the Penæaceæ the sac is quadri-polar, may be a consequence of its spherical or nearly spherical outline in these forms.[4]

On the other hand it may be urged that the embryo-sac varies so very little in its ontogeny, and its contents are usually so markedly differentiated, that it is hard to see, in the large number of cases where a megaspore row is not formed, how four megaspores can have germinated within it, without the normal number and arrangement of the nuclei being disturbed. This is especially so if we regard the sixteen-nucleate sacs mentioned above as cases where this has happened, for in *Peperomia* the nuclei are irregularly distributed, and in the Penæaceæ the sac is quadri-polar. It is difficult to see how a similar result has been avoided in cases such as that of the Liliaceæ, where tetrad-formation may be partially or entirely suppressed within the limits of a single order without apparently influencing the development of the embryo-sac.

3. There are cases in which any one of the megaspore row may function[5]; cases in which more than one megaspore may develop[5]; cases in which no walls are formed between the four megaspore nuclei, so that they are enclosed within a single cell though only one develops[5]; and one case *(Crucianella)*[6] in which the megaspore nuclei thus enclosed in the mother-cell each divide once, the nuclei derived from the micropylar megaspore-nucleus then forming the embryo-sac, while the others degenerate. All these indicate the possibility of four megaspores becoming enclosed and germinating equally within the one mother-cell.

Against this it may be pointed out that whenever a tetrad of

[1] McAllister, 1909, p. 212.   Brown, 1908, p. 456.
[2] Strasburger, 1894 ; Farmer and Moore, 1907, p. 196 ; Ernst, 1908 (B), pp. 26-29.
[3] Němec, *ex* Coulter & Chamberlain (03), p. 74.
[4] Brown, 1908.
[5] Coulter and Chamberlain, 1903, p. 76-87.
[6] Lloyd, 1902, *ex* Coulter and Chamberlain, 1903, p. 86.

megaspores is formed, it is almost invariably the one at the chalazal end of the embryo-sac that develops,[1] while the others degenerate, and there is no adequate reason why this arrangement should be reversed and all four megaspores germinate together to form the embryo-sac in the many cases where this tetrad is suppressed.

4. In *Peperomia*, cell-plates or evanescent cell-walls are formed between the nuclei in the first two divisions, indicating that they should be regarded as nuclei of once-walled spores.[1] Exactly similar, and very suggestive in this connection, is the case of *Smilacina*, where four walled megaspores are formed, arranged in a row or tetrahedrally, and then their division walls are absorbed, so that the megaspore-nuclei occupy a common cell-cavity. In *Smilacina stellata*, each megaspore nucleus then divides once, and the resulting eight nuclei group themselves to form an embryo-sac of the usual type. In *Smilacina racemosa*, the two lower megaspore-nuclei do not divide, but the two upper each divide twice, and the resulting eight nuclei similarly organise the embryo-sac. This fact strongly suggests that the first four nuclei formed in the embryo-sac, in other cases where no walled spores are formed, are themselves spore-nuclei; and similarly that when the mother-cell has only divided once and the embryo-sac originates from one daughter-cell, the two nuclei formed by the first division within this embryo-sac (the homotype division) are the nuclei of two spores.

On the other hand, cell-plates or walls are not reported for the reduction-divisions of the other sixteen-nucleate forms. Moreover, " an evanescent cell-plate is frequently observed during the three free nuclear divisions by which the eight-nucleate stage of the embryo-sac is reached,[2] " and the occurrence of such plates cannot be considered as a criterion of whether the nuclei between which they form are those of spores.

In this brief review, many of the arguments and supporting details used by the upholders of both sides of the question have had to be omitted. Even so, enough has been said to show the difficulty of proving or disproving either view in the present state of our knowledge of the embryo-sac. On the whole, it may be said that the trend of the majority of recent papers is either to leave the question open, or to maintain Coulter's theory.[3] This theory certainly appears to throw light on certain hitherto obscure deviations from the normal type of Angiosperm embryo-sac. Thus it may be held to elucidate the anomalous embryo-sacs described by Campbell in *Aglaonema commutatum*[4] and *Nephthytis Liberica*[5] (species of the Araceæ). In these forms, the number of " sporogenous cells " is variable; each " sporogenous cell " is a potential embryo-sac, and usually more than one begin to develop. The number of nuclei in the mature embryo-sac may be increased to " at least fifteen," their polarity is imperfectly marked, multiple nuclear fusions are seen, and the usual structures of the embryo-sac are not clearly differentiated. It is significant to note that Campbell observes of one species " it looked sometimes as if the structures present at the time of fertilization were the combined products of two or more of the primary embryo-sacs[6] " —and again of the other

[1] Brown, 1908. [2] Coulter and Chamberlain, 1903.
[3] See however Campbell, 1909. [4] Campbell, 1903. [5] Campbell, 1905.
[6] *Ibid*, p. 339.

"it is quite impossible sometimes to be certain whether the structures present at the time of fertilisation are the products of a single embryo-sac, or of two." [1] These facts, in conjunction with Campbell's figures (notably those in which several young embryo-sacs form a linear row), strongly suggest that the "sporogenous cells" are the products of the division of one or more megaspore-mother-cells, and that cases where an increased number of nuclei are seen, result from the germination of more than one spore to form a single embryo-sac.

There remains to be considered one more set of results, which all writers fortunately agree in regarding as revealing reduction-phenomena. Two cases have been described in which there are only two free nuclear divisions within the embryo-sac, which thus contains only four nuclei. One is that of the orchid *Cypripedium*[2], where two of the nuclei form cells round themselves and function as the egg and an attendant synergid, while the remaining two form the primary endosperm nucleus. (In this case the mother-cell divides only once; so according to Pace, who holds Coulter's view, two megaspore-nuclei are included in the sac, each of which divides once). The other case is that of three genera of the order Onagraceæ[3], where three of the nuclei group themselves as an egg-apparatus, while the fourth functions as the primary endosperm nucleus. Here the embryo-sac is one of a row of four megaspores, and it may be remarked that if each of these megaspores were to germinate thus and become included in the one embryo-sac, the result would probably be a sac such as is seen in the Penæaceæ. Another case which may be noted here is that described in two genera of the Podostemaceæ by Went.[4] In these, the mother-cell divides once; the upper daughter-cell then degenerates, and the lower divides again. Those who hold Coulter's view will consider that the two nuclei formed by the latter division are those of two megaspores, and this explanation is supported by their behaviour, for the lower one shrinks to a shapeless chromatin mass, while the upper divides to form a four-nucleate embryo-sac. Went, however, considers that both these nuclei belong to the embryo-sac, and that the division which forms them is the first in the sac. Of the four nuclei produced by the division of the upper nucleus, three form an egg-apparatus and the fourth degenerates so that no endosperm is formed. In *Limnocharis*[5] and *Helosis*[6], (in both of which, it may be significant to note, no row of spores is formed), after the first division in the mother cell the upper nucleus divides twice to form the egg-apparatus and single primary endosperm nucleus, while the lower nucleus quickly degenerates.

It is apparent that all the Angiosperm embryo-sacs which have hitherto been regarded as primitive are now under suspicion. The discovery of an undoubtedly primitive type of embryo-sac—a type which, to satisfy all workers, would need to show more than five successive nuclear divisions from mother-cell to egg—would be especially welcome at the present time, when an important new hypothesis waits to be tested. It is difficult to know where to look for such a sac, as most of the genera which on other grounds might be considered as primitive have already been investigated.

[1] Campbell, 1903, p. 671.   [2] Pace, 1907.   [3] Modilewski, 1909.
[4] Went, 1908.   [5] Hall, 1902.   [6] Chodat and Bernard, 1900.

It should be remembered, however, that reduction and speciali-
sation in other characters need not necessarily imply a similar
reduction in the embryo sac, so that the search should not
be confined to families which are regarded as primitive in other
respects. Thus although it is now generally considered that Mono-
cotyledons have been derived from Dicotyledons,[1] they must have
originated a long time ago, and it may well be that some of them
may preserve ancient characters which have disappeared from
existing Dicotyledons—especially as specialisation in vegetative
characters, such as we find in Monocotyledons, tends to arrest
development of the other organs.[2] On the whole, one can only say
that the wider the range of the search, the greater the chance of
success.

[1] Sargant, 1908, etc.
[2] My thanks are due to Miss Sargant for this suggestion.
Campbell's work on *Pandanus* (Campbell, 1909), may be
mentioned in this connection ; it is too incomplete to have
been taken into consideration in the general discussion.

Botany School,   E. L. STEPHENS
         Cambridge.   (Newnham College).
November, 1909.

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BRITISH LOCAL FLORAS.

"A Tourist's Flora of the West of Ireland." By R. L. Praeger. pp. xii. + 243. Five coloured maps, 27 plates, 17 text figures. Price 3/6. Dublin, 1909.

"The Botany of Worcestershire. An Account of the Flowering Plants, Ferns, Mosses, Hepatics, Lichens, Fungi, and Freshwater Algæ, which grow or have grown spontaneously in the County of Worcester." By J. Amphlett, M.A., S.C.L. (of Clent) and C. Rea, B.C.L., M.A., with the assistance of many friends. The Mosses and Hepatics contributed by J. E. Bagnall, A.L.S. pp. xxxi. + 654. One map. Price 21/- Birmingham, 1909.

"Flora of Cornwall. Being an Account of the Flowering Plants and Ferns found in the County of Cornwall, including the Scilly Isles." By F. H. Davey, F.L.S. pp. lxxxviii. + 570. Six portraits, one map. Price 21/- Penryn, 1909.

Of the books before us, that by Mr. Praeger is the least pretentious and the most interesting. Mr Praeger divides his book into three parts—(i) an introduction, (ii) a topographical section, and (iii) a systematic section. The introduction contains a short description of the physical features of the district, of its climate, of its vegetational sub-divisions, of its plant communities, and of the character of its flora. As showing the remarkable luxuriance of plants which are sheltered from wind, we are informed that *Asplenium marinum* may be seen with fronds three feet in length, that *Ceterach officinarum* attains a length of one foot, and *Adiantum Capillus-Veneris* and *Polypodium vulgare* of nearly two feet; yet, on the whole, exposure is so great that woods are very rare, and agricultural operations in West Mayo and West Galway are only carried on up to an altitude of 400 feet. Mr. Praeger draws attention to the well-known species of the "South-west European group," such as *Arbutus Unedo, Pinguicula grandiflora, Erica mediterranea, E. Mackaii,* and *Daboecia polifolia,* and to those of the "American group," such as *Sisyrinchium angustifolium, Eriocaulon septangulare* and *Naias flexilis.*

In discussing the origin of these groups in Ireland, the author says that "any other theory than that of land-migration seems out of the question." We are sure that many readers of Mr. Praeger's excellent little book will not subscribe to this opinion, which follows on the lines of Forbes, and more recently of Dr. Scharff and Professor Carpenter. Similarly, many readers will, we may be certain, dissent from the view that the "South-west European group" of species in Ireland is a vestige of the Tertiary flora.

The "systematic section" occupies about half of the book, and is a flora of the accepted type. So far as one can judge, it appears to be a very accurate compilation of the species which have been recorded from the author's chosen area. Certain genera, such as Rubus, receive such detailed treatment as to render some portions of the book unintelligible to ordinary field botanists, as the "species" are not arranged in groups. On the other hand, some genera receive scant justice from the standpoint of "elementary species." For example, of the genus Salicornia only one "species" is recorded, namely *S. herbacea,* a name which

has no definite significance. This irregularity of treatment is, of course, unavoidable in any local flora. The only adverse criticism we have to make regarding this section refers to the so-called common names used by the author. We should not have thought that anybody found such names as " Bristle-leaved Spike-rush " easier to remember or in any way more useful than *Scirpus setaceus.* In the matter of nomenclature, the book is admittedly old-fashioned. Mr. Praeger refuses to follow any one of the three recent catalogues of British plants on account of their nomenclatorial discrepancies. "We in Ireland," says the author, "dwell remote from the exhilarating sport of name-changing;" but we think it a pity that a few of the leading rules of the Vienna Congress were not adopted.

The area included under the term "West of Ireland" has been chosen so as to join up Donegal in the north with Kerry and Cork in the south; and thus the district of Killarney is excluded.

The book more than fulfils the purpose for which it was written, namely, to serve as a 'first aid' to the tourist who desires information in a condensed form respecting that peculiar flora " of the West of Ireland." It is beautifully and profusely illustrated with excellent photographic views of the more interesting plants, with excellent coloured maps, and with small, but particularly useful, sketch maps. The price of the book is, considering all these points, extraordinarily low; and we hope and expect that the book will have a correspondingly large sale. If a new edition is called for, we hope the three indexes will be merged into one and placed at the end of the book. Multiple indexes are always vexatious, more especially when, as in the present case, they are placed in different places in the general body of a book.

"*The Botany of Worcestershire*" is a high-priced and portentous work. There is a short introduction which gives us an incomplete account of the physical features of the county. There is no account of the soils (as opposed to the geological strata), and no general account of the vegetation of the district. In these respects, the flora is distinctly inferior to those on more modern lines, such as Crump and Crossland's Flora of Halifax, and Wheldon and Wilson's Flora of West Lancashire. The "botanical districts" are, from the point of view of vegetation, quite artificial and follow conventional lines in being named after rivers. The book records the occurrence in Worcestershire of 1146 species of Angiosperms, 3 Gymnosperms (placed between the Monocotyledons and the Dicotyledons), 36 Pteridophytes, 7 members of the Characeæ (placed between the Pteridophytes and the Musci), 369 Bryophytes, 171 Lichenes, 1399 Fungi, and 65 Algæ, giving a grand total of 3196 species. Without doubt, this represents an extraordinarily large amount of field-work on the plants of Worcestershire, and in the performance of this work much information of an interesting and valuable nature must have been acquired with regard to the biology of the various species. This useful information is, however, carefully hidden in the mere listing of names and localities. In the section dealing with the flowering plants and ferns, " particulars about the plant which the writers think may be useful or interesting " are given. We give one of such items which appears under *Clematis Vitalba.* "The plant is an irritant, but the young shoots are edible; in some places the

branches are used for making baskets, and the leaves as fodder for cattle; while boys smoke the dried stems." In many cases, the authors give distinguishing characters for closely allied species; but it would appear that, in a number of cases, the distinctions are simply taken from the standard floras. Many of the distinctions given are faulty or worthless, as with regard to the oaks, the birches, the elms, the poplars, the gentians, the primulas, and many others. The book is accompanied by a map showing the "botanical districts" and the gains and losses in area to the county since 1832. The title of the book is, of course, in imitation of Edwin Lees' "Botany of Worcestershire." Whilst such a title was perhaps admissible in 1867, it is rather an affectation to use it to-day.

The "*Flora of Cornwall*" limits its records to flowering plants and ferns. A useful introduction gives short accounts of the topography of the district, the climate, the geology, a "history of botanical research in Cornwall," the "botanical districts," a list of books, manuscripts, herbaria, etc., quoted, and a capital statistical summary. The flora records 1180 species, of which 953 are said to be natives, 64 colonists, 46 aliens, 16 casuals, and 101 "denizens." This classification is said to be in accordance with the plan formulated by H. C. Watson; but as in the case of the Botany of Worcestershire, the term "denizen" is used in a sense quite different from that of the precise definition given by Watson, who would not have considered *Lycium chinense* and *Omphalodes verna* as denizens but as aliens. H. C. Watson defined a "denizen" as a plant only "liable to some suspicion of having been originally introduced;" whereas an "alien" is one which has been "presumably introduced." "In the following table" (p. lxxx.), "a comparison is instituted between the types of distribution occurring in Great Britain as a whole, and in Guernsey and Cornwall respectively. The figures for Guernsey are taken from Mr. Marquand's flora of that island":—

Types.	Gt. Britain.		Guernsey.		Cornwall.
British ...	532	...	394	...	515
English ...	409	...	179	...	286
Scottish ...	81	...	2	...	16
Intermediate	37	...	0	...	7
Highland ...	120	...	0	...	0
Germanic ...	127	...	18	...	28
Atlantic ...	70	...	38	...	60
Local or doubtful	49	...	5	...	0
Totals	1425	...	636	...	912

The following twenty plants occurring in Cornwall are "not recorded for any other county in Britain":—

Allium Babingtonii.
A. sibiricum.
Artemisia stelleriana.
Bromus maximus.
Chara fragifera.
Echium plantagineum.
Erica vagans.
Fumaria occidentalis.
Herniaria ciliata.
Juncus capitatus,

Juncus pygmæus.
Lavateria cretica.
Narcissus odorus.
Nitella hyalina.
Ornithopus pinnatus.
Pinguicula grandiflora.
Scabiosa maritima.
Trifolium Molinerii.
T. Bocconi.
T. strictum,

The author does not state, however, that at least one-third of these are not indigenous to the county.

On the whole, the Flora of Cornwall is a straightforward and useful account of the plants of Cornwall; and the book, although expensive, will be extremely useful to a large number of people who wish to herborize in one of the most interesting parts of Britain.

C.E.M.

FUNGI.

"RESEARCHES ON FUNGI," by A. H. Reginald Buller, Professor of Botany at the University of Manitoba, pp. XI. + 287. Longmans, Green & Co., London, 1909. Price, 12/6 net.

IN a subsidiary title the author explains that the present volume comprises "an account of the production, liberation, and dispersion of the spores of Hymenomycetes treated botanically and physically, also some observations upon the discharge and dispersion of the spores of Ascomycetes and of *Pilobolus*." By far the greater part of the book is concerned with the sporophores of Hymenomycetes which are primarily considered from the point of view of spore discharge. The author's own researches along these lines are well known. This book collects together much of the previous work done by Professor Buller and a considerable quantity of hitherto unpublished material. Its publication indicates a distinct advance in our knowledge of the higher fungi.

In the opening chapters of the book the author discusses the efficiency of the sporophores of the Hymenomycetes as organs for the formation and liberation of enormous quantities of spores. He makes some interesting calculations to show what a large relative increase of hymenial area is given by the production of gill plates in the Agaricineæ and of spores in the Polyporeæ. He points out also the necessity for stability of the fructifications of these groups if spore-discharge is to be effected efficiently, for, were the pileus of a mushroom *e.g.*, allowed to sway to and fro, very few of the spores would be able to fall free from the gill plates.

One of the most instructive parts of the book is undoubtedly that dealing with the correlations made by Professor Buller between the reactions of the fruit bodies of the Hymenomycetes to external stimuli such as light and gravity on the one hand and the general structure and habitats of these fungi on the other. Thus the development of the fruit bodies of *Lentinus lepideus* is affected both by light and by gravity, while the fructifications of the common mushroom (*Psalliota campestris*) react only to gravity. The former fungus grows on wood and its orientation to the substratum is indefinite, so that heliotropic curvature of the stipe would be of obvious advantage. On the other hand the mushroom in nature grows on the ground, the surface of which is generally horizontal over a limited area; thus heliotropic reaction in this case is unnecessary. The author correlates also the heliotropism exhibited by many coprophilous fungi (e.g., *Coprinus*, *Pilobolus*) with the irregular surface of the substratum on which they grow.

The spore cloud of *Polyporus squamosus* is then described, a phenomenon which, it may be said in passing, is extremely striking to one viewing it for the first time. Similar spore clouds have

been shewn by Buller to be discharged from mushrooms and allied fungi by the employment of a concentrated beam of light below the sporophores at the time of maturity.

Some interesting observations are recorded which deal with the power possessed by genera such as *Schizophyllum*, *Polystictus*, etc., of withstanding dessication without injury. When the dry fructifications of *Schizophyllum commune* are damped, spore discharge is almost immediately resumed.

The author brings forward evidence which shows that the basidiospores of Hymenomycetes are shot violently from their sterigmata, though the mechanism of this process is still obscure. A large amount of work has been done on the physics of spore-fall and this botanist has applied for the first time a direct test of the applicability of Stokes' Law to the fall of microscopic spheres in air.

Another interesting feature of the book is the new light thrown by the writer upon the Coprinus type of fruit body, in which, as is well known, the gills deliquesce at maturity. It has often been supposed that the spores fall into the liquid thus produced and that insects seek this liquid and so effect the dissemination of spores. Buller puts forward the view that the process of deliquescence is one of auto-digestion which enables successive parts of the gills to liberate their spores effectively, because it is found that in the Coprinus type of fruit body all the basidia over a small area of a gill are mature at the same time. It certainly seems that the author has put forward a more adequate explanation of this phenomenon of deliquesence than has previously been given.

The observations on spore discharge in Ascomycetes are less detailed than those previously discussed, and few new results are recorded.

A useful summary of the successive chapters is given at the end of the book. The figures and photographs are clear and the letterpress is excellent.   F.T.B.

"THE GENERA OF FUNGI," by F. E. Clements, Ph.D., Professor of Botany in the University of Minnesota. Minneapolis, 1909.

THE aim of this book is to provide a key for the identification of the genera of Fungi. The author, who is well known as an ecologist, states in the preface that the book is an outgrowth of a translation of the keys in the early volumes of Saccardo's "Sylloge Fungorum" for the use of students of mycology. A suitable book of this type would be of considerable utility to those commencing the study of Fungi, but the author of the volume under consideration has such extraordinary ideas in regard to the classification of the Fungi that the use of the book cannot be recommended. One recognises, of course, that "keys," in themselves do not necessarily indicate natural relationships, but there seems to be no justification for the inclusion of the Bacteria in the Phycomycetes and of the Uredineæ in the Ascomycetes! Concerning the latter, Professor Clements considers a sorus of teleutospores to be an apothecium, the teleutospores corresponding to asci with fixed spore cells. What is there to be said for such a view as this?

F.T.B.